SCHULTES, SYNOPSIS OF HERRANIA 1958]

217

A SYNOPSIS OF THE GENUS HERRANIA

RICHARD EVANS SCHULTES

With seventeen plates

La flor se podrá mirar como la mayor maravilla del reino vegetal, y apenas se pudiera creer que la económica y sencillísima naturaleza hubiese gastado tantas cintas y atavíos para engalanarla casi con la ostentación de las modas.

- Eloy Valenzuela (1784)

MORE THAN AN ACADEMIC INTEREST moves me to present this study of the sterculiaceous genus Herrania, a close relative of Theobroma, the genus of the cultivated cacaos. In recent years, the chocolate industry of the world has become increasingly alarmed over the ravages of certain fungal and virus diseases of the cultivated forms of Theobroma. These are so serious that the industry has waned almost to extinction in several parts of the world, and our sources of certain grades of chocolate are seriously threatened. Extensive investigations toward a control of the disease have been carried out in a number of scientific institutions; much has been done in plantations toward selection of resistant strains, and several attempts to do this from wild material have been made; furthermore, attention has been devoted toward the possibility of overcoming the difficulties through hybridization and other techniques.

It is my belief, however, that sooner or later an extensive program for selection of new germ plasm from the jungle must be initiated, if the chocolate industry is to be saved. Naturally, such a project would include all near allies of Theobroma (Schultes, R. E. "El género Herrania, pariente silvestre del cacao cultivado." Agric. Trop. 7: 43-48. 1951; "Le genre Herrania, parent sylvestre du cacaoyer cultivé." L'Agron. Trop. 6: 661-663. 1951). In 1952-53, the Imperial College of Tropical Agriculture in Trinidad and the Colombian Ministerio de Agricultura carried out jointly a very thorough study of Theobroma and Herrania in the Amazonian sector of Colombia. This study, which was headed by the late Prof. Richard E. D. Baker and Dr. Francis W. Cope, of the Imperial College, and which included half a dozen additional British and Colombian scientists, explored many of the major rivers of the region and made selections of interesting or outstanding material for the cacao-improvement scheme in Trinidad.

Herrania first attracted my attention in 1941, when I collected a then undescribed species in southern Colombia. The process of determining and describing this collection brought out the great need for a revisionary treatment of the genus. Nevertheless, in view of the sparse and fragmentary collections then in our herbaria, as well as the unavailability during the war of material from European institutions, it seemed advisable to await a more favorable time before undertaking such a revision.

From 1941 to 1953, I was engaged in almost uninterrupted field studies (chiefly of the genus Hevea) in the Amazon Valley. In connection with this work, it was often possible for me to give special attention to Herrania in its native habitat and to make collections over a wide area. This intimate association with the living plants enabled me to study a number of morphological and ecological characters which are lost in the preparation of herbarium material. It has also been possible, in some cases, to study and collect fruits which, although often wanting in our herbaria, can be highly significant from the taxonomic point of view.

In addition to field studies, I have consulted all available specimens from the principal herbaria in the United States and South America in the preparation of the following synopsis. Furthermore, in 1947 and again in 1950, I was able to study the collections preserved in England and on the continent of Europe.

Although it would seem that sufficient material upon which to base an admittedly preliminary treatment of Herrania has now been consulted, we must realize that certain concepts are still rather poorly understood. Further field studies will almost certainly lead to alterations in our present treatment and will undoubtedly enhance our knowledge of the composition and geographic distribution of the genus.

ACKNOWLEDGEMENTS

So many friends have aided me in so many ways in both the herbarium and the field that I find it difficult to thank them all individually. The late Professor Oakes Ames, of Harvard University, followed my field and herbarium investigations of Herrania from their beginning and, by letter and conference, stimulated me with his many suggestions and with his deep interest in economic botany. It is with warm appreciation that I thank Professor Paul C. Mangelsdorf, director of the Botanical Museum of Harvard University, for his constant encouragement in the work of preparing this study of *Herrania*. My colleagues at the Botanical Museum, especially Dr. Albert F. Hill and Mr. Charles Schweinfurth, have likewise given generously of their time, advice and encouragement throughout the years of preparation of this study. My deep gratitude must go to Dr. E. W. Brandes and Dr. Robert D. Rands, who directed my work on Hevea rubber for the United States Department of Agriculture, for their encouragement and understanding of my botanical activities which, like the Herrania investigation, were not directly concerned with my regular studies in latexbearing plants. Dr. N. Y. Sandwith of the Royal Botanic Gardens, Kew, has been most generous with his help during the last few years of this study. To Dr. Armando Dugand, former director of the Instituto de Ciéncias Naturales in Bogotá, and Dr. Felisberto Camargo, former director of the Instituto Agronômico do Norte in Belém do Pará, Brazil, I am especially indebted for their interest and for many kindnesses during my years of field work. Mr. Gordon W. Dillon, the late Señorita Inés de Zulueta and Miss Helen Schieffer deserve my warmest thanks for their drawings which were published in some of my earlier taxonomic papers on Herrania.

It is difficult for me to express adequately my gratitude to Mr. Elmer W. Smith for the highly accurate and artistic drawings which illustrate this synopsis. Sincere thanks go also to the American Cocoa Research Institute and the National Science Foundation for generous grants of money towards the illustrating of my taxonomic studies in this genus of close relatives of the chocolate plant.

My deepest appreciation is due to the numerous members of the Anglo-Colombian Cacao Collecting Expedition, especially to the late Prof. Richard E. D. Baker and to Dr. Francis W. Cope, together with which Expedition I was able to spend many months in the field and to test the workability and completeness of this synopsis of *Herrania*.

To the directors and staffs of the following American botanical institutions I send my thanks for the loan of specimens or for their kind permission to consult material in their care; the Gray Herbarium, the Arnold Arboretum, and the Economic Herbarium of Oakes Ames (Harvard University); the Bailey Hortorium (Cornell University); the New York Botanical Garden; the Missouri Botanical Garden (St. Louis, Mo.); the Chicago Natural History Museum; the United States National Herbarium (Washington, D. C.); the United States National Arboretum [Herbarium] (Beltsville, Md.); the Philadelphia Academy of Natural Sciences; and the Yale School of Forestry (New Haven, Conn.). I am deeply grateful also to the officers of the following European and South American botanical centers for their many courtesies during my periods of study in their herbaria; the Royal Botanic Gardens (Kew) and the British Museum (Natural History) (London); the Botanisch Museum en Herbarium (Utrecht); the Rijksherbarium (Leiden); the Universitats Botaniska Museum (Copenhagen); the Museum National d'Histoire Naturelle (Paris); the Jardín Botánico (Madrid); the Conservatoire Botanique (Geneva); the Herbier Boissier (Geneva); Jardin de l'État (Brussels); the Botanische Staatssammlung (Munich); the Naturhistoriska Riksmuseum (Stockholm); the Instituto de Ciéncias Naturales (Bogotá); the Facultad Nacional de Agronomía (Medellín); the Instituto Agronômico do Norte (Belém); the Museu Goeldi (Belém); the Jardim Botânico (Rio de Janeiro); the Instituto Miguel Lillo (Tucumán); and the Instituto Interamericano de Ciéncias Agrícolas (Turrialba, Costa Rica).

HISTORICAL NOTES

Herrania was described by Justin Goudot in 1844 and was named in honor of General Pedro Alcántara Herrán (1800–1872), president of New Granada (Colombia) from 1841 to 1845. In spite of civil unrest in the country, Herrán showed much interest in the botanical investigations of Colombia during this period. It is therefore quite appropriate that this genus, which has its center of diversification in Colombia, should bear his name.¹

¹ It is equally appropriate for me to express, in this paper, summarizing our present knowledge of *Herrania*, my gratitude to Dr. Alvaro Herrán Medina, his great grand-

The specimens upon which this genus and its first two species, Herrania albiflora and H. pulcherrima, were based had been brought to the attention of the scientific world long before the actual publication of the genus in 1844. At the meeting of the Linnean Society of London on January 15, 1828, Goudot referred to "a plant of the genus nearly akin to Theobroma from which it differs chiefly in habit, in the form of the calyx, and the structure of the stamens . . . 'Arbuscula foliis digitatis, quinatis'" (Philosoph. Mag. 3: 132. 1828). Before presenting his diagnosis of Herrania, Goudot devoted much careful study to the new genus, for he wrote "[since 1828] . . . I have had frequent occasions to study these plants and to assure myself that they ought to constitute a distinct genus" (Ann. Sci. Nat. Paris III. 2: 229. 1844). Goudot's original diagnosis of Herrania, reproduced below, is so detailed and so carefully prepared, with such a clearly outlined concept as to relationship, that now there is no need to alter either the description or the concept, and this in spite of the fact that the number of species known has been measurably increased. Long before Herrania was actually described, however, several species were recognized as distinct from Theobroma. The Botanical Expedition of Mutis in New Granada (Exped. Bot. Mutisii Novae-Granat.), which was carried out in Colombia by a capable and devoted group of scientists under the leadership of Padre José Celestino Mutis from 1783 to 1808, collected some 4055 specimens, including several species of Herrania. The greatest heritage of the expedition is the collection of water-color paintings of Colombian plants, numbering 6900 plates and representing 2800 species. The plates, in perfect condition, are preserved in the Jardín Botánico in Madrid and their publication has only recently been initiated. I was fortunate in 1950 to have an opportunity to study many of these plates, but permission to publish any of them could not be granted. Amongst the 6900 plates, there are several extraordinarily artistic and accurate illustrations representing three species of Herrania. These plates, labelled simply "Theobroma" by the artists, are all included in Volume No. 28 under number 5333. They were first determined as representing several concepts of Herrania by Triana, who annotated each plate in pencil and signed his annotations. These plates were made about half a century before the genus Herrania and the three species so beautifully represented by the Mutis plates were described by Goudot.

Recently, a most significant discovery related to the work of the Mutis Expedition was made. The Colombian historian, Dr. Guillermo Hernández de Alba uncovered, in 1950, a beautifully preserved manuscript prepared by Padre Eloy Valenzuela, one of the most active members of the Expedition. The manuscript is without title, but Dr. Enrique Pérez-Arbeláez entitled it "Diario de la Expedición Botánica del Nuevo Reino de Granada

nephew, and my good friend. Dr. Herrán Medina, who served for a number of years as Colombian Consul General in Manáos, Brazil, followed the progress of my work in the Amazonian area of both Colombia and Brazil with enthusiastic interest and performed innumerable services and favors without which that work would have been much more difficult.

dirigida por Don José Celestino Mutis y llevado por Eloy Valenzuela desde el día 29 de abril de 1783 al día 8 de mayo de 1784" (Pérez-Arbeláez, E., Un hallazgo histórico y científico: el diario de D. Eloy Valenzuela. El Tiempo (Bogotá), February 11, 1951). Thanks to Dr. Pérez-Arbeláez, I may quote in full this extraordinarily detailed description of a species of Herrania which Valenzuela wrote in his diary and publish a photograph of one of the pages in Valenzuela's own hand. This description, referring without doubt to Herrania pulcherrima, is the earliest reference to Herrania of which we have any knowledge. In it, Valenzuela clearly sets forth his recognition of the plant as different from the cacao común (Theobroma Cacao). Goudot's validly published diagnosis and description of Herrania is, for all practical taxonomic purposes, the earliest; but, for historical reasons, I am publishing herewith a transcript of Valenzuela's diary-notes on his cacao esquinado. There is every reason to believe that the plant to which these notes refer grew in the vicinity of Mariquita, where the Expedition carried out a great part of its labor.

Día 13 de marzo de 1784. Sin concluir el Guácimo real, se trabaja hoy en el cogollo de la theobroma de cintillas o Cacao esquinado. El otro día repetí mi visita a la mata y el dueño me dijo que los cuatro tallos que tiene aproximados corresponden a una raíz sola. Los tallos serán hacia el pie tan gruesos como el dedo pulgar sin ramo alguno tupidísimos juntamente con las hojas de pelo chico, apelmazado y amonado; por dentro blanco, fibroso, ligeros; la parte leñosa es radiada con líneas que tiran para el centro; el meollo gruesesito, blanquísimo, esponjoso, regado de puntos lucientes y cercado con algunas fibras huecas. Una de estas partes despide algo de un licor diáfano y viscido. Hojas son alternas bastante inmediatas, patentes, decusadas. — Estípulas dos laterifolias algo retiradas opuestas adpressas, subuladas pollicares y de la misma pubescencia que el tallo y hojas. — Flor: agregadas axilares y supraaxilares, peculiares de la parte inferior; pedícelos sencillos, recurvos o levantados para arriba.

Día 14. Domingo.

Dia 15. Se trabaja en dibujar el tallo del cacao esquinado o theobroma de cintillas en la parte que carga las flores y como vinieron muchas de éstas, he tenido lugar de hacer el apunte casi por entero.

Cacao Esquinado. Raíz. Tallo: De la altura humana, derecho, rollizo, sencillísimo, tupidísimo de pelo chico, grueso al tanto del dedo pulgar: y parece que acompañado de 3 a 4 sobre una raíz; su color parduzco sucio, hacia el pie es algo desnudo y color de café y aquí mismo tiene la epidermis menudamente hendido-reticulada y algo levantada. — La corteza es gruesesita, verdosa debajo de la epidermis y flexibilísima, el interior blanco, fibroso, ligero y en el corte transversal se ve radiado con rayas que tiran al meollo desde la misma corteza: este es blanquísimo bofo y cercado de orifícios capilares por donde mana un jugo muy cristalino y gelatinoso.

Hojas: Grandes, alternas, túpidas, de pelo chico, 1-partidas hasta el mismo pezón común. — Pezón: común: patentes, pedales, multisulcados a lo largo y geniculados en los extremos. — Hojuelas: cuneiformes en la mitad inferior, escabradas por encima, membranáceas, y de bordes enteros, regados de puntas rigidiúsculas; la mayor excede al pezón común: las anteriores chicas obovato-

oblongas, obtusas con punta: las exteriores se ensanchan desde la mitad y abren en lacinias pinnadas, anchas, acuminadas, de las que son más grandes las dos primeras, más anchas las 3 terminales. En algunas hojas se suele añadir una chica y roma antes de las primeras. — Venas: paralelas, rectas, distantes. — Estípulas: 2 laterifolias, algo distantes de la axila, subuladas adpressas, pollicares y conformes a la extensión del tallo.

Flor: amontonadas, túpidas, axilares y supraaxilares en la parte inferior del tallo y casi siempre en las axilas desnudas, pollicares ligeramente olorosas y de color purpúreo, o bien de carmín profundo. — Pedúnculos: ningúnos. — Pedícelos: sencillos, levantados, delgadisimos por el pie y con dos o tres subulas cortas. --Cáliz: periantio monófilo, coriáceo, colorido, paludo exteriormente; antes de abrir es cerrado, ovado, obtuso; no se divide hasta cerca de la base en 3 partes cóncavas, enteramente reflexas, semipollicares; la una aguda; las dos anchas y agudamente semibífidas; parece que por su naturaleza es semiquinquéfido agudo y que al reflectar se hiende algo más, y no se apartan algunas veces los tres segmentos. Nectarios: de 5 piezas, subrotundas, chicas, convexas exteriormente, embroscadas hacia adentro, plegadas y venulosas longitudinalmente y puestas alrededor del receptáculo: sus apéndices: son otras tantas cintillas angostas lineares, con 6 pollicares corridas a lo largo de dos o más venitas de color más subido. Antes de abrir están envueltas en piezas paradas sobre los pétalos y el color tira al amarillo.

Corola: de 5 piezas alternas con las del nectario y más interiores, lanceoladas, derechas, patentes de una longitud con el periantio, surcadas por encima a lo largo y cuadunadas ligeramente en la base.

Estambres: de 10 filamentos nacidos del lado de los pétalos, cortados, gruesos, recurvados para afuera, apareados y aproximados por los apices; anteras lineares, univalves, rayadas a lo largo, convexas, adnatas, a otras tantas lacinúlas de los filamentos, blancas y escondidas en el seno de los nectarios; 4 están en un filamento y 2 en el lateral. Estas forman como un ángulo y las primeras forman dos, metido el uno en el otro.

Gérmen: superior, pentágono, pyramidal, hirsuto, chico, de color herbáceo. — Estilo único linear, subduplo de la altura de los pétalos. — Estigma un poco obtuso y parece sencillo.

Fruto: bayas sentadas sobre la flor marchita, o bien mazorca ovada acuminada, tripolicar, 5 angular verde lustrosa y regada de tomento caedizo; el acumen es entero algo oblícuo; los ángulos levantadísimos, anchos, enteros, sólidos, venulosos lateralmente y alternan con 5 venas gruesas, algo anguladas, extendidas longitudinalmente por la depresión de ellos; la corteza blanda quebradiza, subglutinosa en la partidura, blanca y destituída de ángulos por dentro. Meollo ovado, 5 surcado, libre de la corteza y prendido por la base. — Granos: 70 convexo-angulados, rugoso-reticulados, coloridos de rosado blanquísimo, arilados con un saco fibroso empapado en jugo agridulce, y aproximados como en 5 hileras con alguna pulpa intermedia. — Receptáculo común, leñoso y central; parciales filiformes.

El interior . . .

El córculus asoma la cabecilla en la superficie interior . . . Cotiledones sin las complicaciones del cacao común.

Hojas seminales:

Tengo puestos algunos granos de tierra húmeda para ver si nacen y con esto determinar el modo con que se explica su interior y el tiempo que se necesita.

SCHULTES, SYNOPSIS OF HERRANIA 1958] 223

Nace con mucha frecuencia en el monte y rozas de esta inmediación: el grano amargo y sumamente mantecoso, dicen ser apetecido y consumido por los micos. La flor se podrá mirar como la mayor maravilla del reino vegetal y apenas se pudiera creer que la económica y sencillísima naturaleza hubiese gastado tantas cintas y atavíos para engalanarla casi con la ostentación de las modas.

El periantio por fuera es de color acanelado, sucio salpicado de carmín, casi borrado. Por dentro es lustroso y de carmín hermoso.

Nectario: en el fondo es blanquecino o descolorido; las venitas y pliegues son de púrpura oscura. Las cintillas son carmesíes con venas oscuras.

Pétalos de púrpura afinadísima sub-oscura.

Estambres: en los filamentos son carmesíes y en las ánteras blancos. Gérmen: pálido verdoso. Estilo purpúrea; estigma blanco. Mazorca verde: por dentro sub-rósea.

Día 16. Se trabaja hoy en la hoja del cacao esquinado.

ECOLOGICAL PREFERENCES OF SPECIES OF HERRANIA

Herrania is distributed from sea level to about four thousand feet, but the altitudinal range of each species is often strictly limited. Herrania purpurea has been collected at sea level, and most of the specimens of this species are from localities below two hundred feet. Herrania Mariae occurs on the great flat Amazon planada from sea level at the mouth of the Amazon River to approximately three hundred and fifty feet in the western parts of the Amazon Valley. Herrania nitida and H. tomentella can be found in the western Amazon and Orinoco drainage-areas, from about two hundred and fifty feet above sea level up to the base of the Andes at about nineteen hundred feet. Herrania albiflora inhabits the slopes of the Andes between about three hundred and three thousand feet, thus exhibiting a more surprising altitudinal tolerance. The only known collection of H. umbratica was taken at about twenty-one hundred feet. Although the type collection of H. pulcherrima was made on the eastern slope of the Colombian Andes at about fifteen hundred feet altitude, most of the other collections are from the central Andean regions at about three thousand feet, with a distinct variety near sea level in western Colombia. Apparently rather intolerant of altitudinal variation is Herrania laciniifolia, which is known only from regions between three and four thousand feet. One of the species which seems to be confined to a narrow altitudinal range is H. breviligulata known from two collections from the eastern slopes of the Andes between eighteen and twenty-five hundred feet. The occurrence of H. Camargoana merits special mention, for it is unknown except in the upper Rio Negro basin of Brazil and Colombia, where it is found near or on the summits of barren granitic mountains rising to an altitude of about five hundred feet above the level of the river (or approximately twelve to seventeen hundred feet above sea level) and, rarely, in sandy riverside savannahs. Herrania Cuatrecasana, H. Dugandii, H. kofanorum and H. nycterodendron appear to be confined to the dense forests of the westernmost parts of the Amazon Valley at an altitude of from three hundred to one thousand feet. Herrania lemniscata is found between four hundred

JOURNAL OF THE ARNOLD ARBORETUM [vol. xxxix and three thousand feet and *H. kanukuensis* between four hundred and one thousand two hundred feet.

The species of *Herrania* do not seem to be exacting in their soil requirements, with the single exception of H. Camargoana which prefers and, actually, is found exclusively on sterile white sand and on the most inhospitable of rocky slopes strewn with granite blocks and often nearly devoid of soil. Most species thrive on well-drained slopes, but I have seen Herrania purpurea in the northwestern part of Colombia along the banks of rivers where, in the rainy season, the plants stand in from four to six feet of water. Similarly, Herrania Mariae often grows in Amazon forest which is subject to deep flooding half the year. Herrania lemniscata is also reported to grow in "mixed forest in swamp and on rather swampy soil" or "en selva anegada en la estacion lluviosa." The widely distributed Herrania nitida, in the Amazon Valley, is found usually just above the reach of the deep annual inundation, although occasionally it occurs where a few feet of water may stand for several weeks; it cannot, however, be classified as a flood-tolerant species. There is one point which stands out in relief concerning the ecology of the various species of Herrania: both in altitudinal tolerance and in topographical preference there is a tremendously wide range within the genus. Some species seem to be extremely exacting, whereas others show an unbelievable tolerance in both altitudinal and topographical distribution. Although all species of Herrania are primarily forest trees, a number act like weeds and propagate rapidly in agricultural clearings. The heliophilic tendency is especially marked in Herrania nitida. In the Amazon area, especially in Indian settlements, trees of Herrania are never sacrificed in the clearing of a field for planting or in the weeding of a cultivated patch. Since most cultivation is attempted on land above the reach of the annual flood, the species most commonly met with under conditions of partial human care is Herrania nitida. The only reason for not cutting down Herrania trees is, apparently, the esteem in which the natives hold the acidulous pulp surrounding the seed. Under conditions of ample room and sunlight, many more fruits mature than in the forest, and man is thereby repaid for his little consideration in sparing the tree. This toleration of the tree in planted fields is undoubtedly the basis of occasional reports that Herrania is sometimes cultivated. I have never seen Herrania under conditions of cultivation, nor have I been able to find reliable reports in the literature or on herbarium specimens to this effect.

USES OF SPECIES OF HERRANIA

As has been pointed out above, the principal importance of *Herrania* lies in its potentialities as a source of new germ-plasm in a possible hybrid-ization program with the cultivated species of *Theobroma*.

In addition to this potential use, a few species find employment among native peoples. Everywhere *Herrania* trees are left standing in cultivated ground, because the white, acidulous pulp in which the seeds are embedded

225

is eaten. Apparently this pulp is most delicious just before complete ripening of the fruit, and for this reason, it is often difficult to find a mature capsule. It is said that monkeys also search for the fruit as a food. Among the Ingano Indians of Mocoa, in the Putumayo of Colombia, the ashes of the bark of Herrania breviligulata are employed to dry up and "cure" infected wounds and ulcers (Schultes & Smith 2050). In British Guiana, according to notes accompanying Archer 2514, Herrania lemniscata is utilized in the preparation of a "beverage like chocolate." Similarly, Pittier reports (Plantas Usuales de Costa Rica. 72. 1908) that the Bribrí Indians of Costa Rica employ the seeds of Herrania purpurea to make a bitter drink. It has been reported (Van Hall, Cacao. ed. 2. 74. 1932) that formerly, in northern Colombia, the seeds of Herrania albiflora were purposely mixed with those of commercial cacao to improve the flavor of the chocolate and that these same seeds were often used to prepare a bitter febrifuge. Herrania Mariae seeds were formerly found as an adulterant in "Pará cacao" (Van Hall, loc. cit.).

RELATIONSHIPS AND TAXONOMY

Herrania appears taxonomically to be intermediate between Guazuma and Theobroma. It approaches Guazuma in the placement of its anthers but has an entirely different habit and fruit. It can be separated from Theobroma immediately by its habit (having compound-digitate leaves and, in general, comprising small, delicate and slender treelets). It further differs from Theobroma in the placement of its stamens, in the number of divisions of the calyx, in the length and form of its ligules, in its wood anatomy and in the structure of the pollen grains. The fruit of Herrania resembles, in outward form, that of Theobroma, but the seeds of Herrania have thick cotyledons which are almost entire and which are apparently not folded. The field botanist has perhaps a better opportunity of noting the differences between Theobroma and Herrania, for, in addition to the technical characters listed above, he is able to appreciate the great difference in habit and to observe that the jorquetting habit of branching, so characteristic of Theobroma, is not found in Herrania.

Although it would appear, on the basis of a taxonomic and morphologic examination of recent collections and field studies, as well as on experimental evidence, that *Herrania* may very justifiably be considered as a genus distinct from *Theobroma*, it has, in the past, usually been relegated to the position of section or subgenus under *Theobroma*. Schumann (in Martius, Fl. Brasil. 12(3): 70–72. 1886), for example, considered Goudot's *Herrania* to constitute merely a section of *Theobroma*, which genus he divided into the two sections: *Herrania* and *Eutheobroma*. Bernoulli (Uebersicht der bis jetzt bekannten Arten von *Theobroma*. 4. 1871), on the contrary, had divided *Theobroma* into four sections but kept *Herrania* as a distinct genus, stating, ". . . *Theobroma* ab *Herrania* Goudot genere proxime affini differt praecipue habitu, foliisque integris nec digitatim quinque- sexfoliolatis."

The general tendency in recent years has been to keep *Herrania* and *Theobroma* as distinct genera. Cook (Contr. U.S. Nat. Herb. 17: 616. 1916), for example, followed this course. Cheesman (The economic botany of cacao. Suppl. Trop. Agric. 1. 1932) pointed to *Herrania* and *Guazuma* as the nearest relatives of *Theobroma*. Chevalier (Révision du genre *Theobroma* d'après l'Herbier du Museum National d'Histoire Naturelle de Paris. Rev. Bot. Appl. Agric. Trop. 26: 265. 1946) excluded *Herrania* from his treatment of *Theobroma*. A recent morphological and taxonomic study of *Guazuma* (Freytag, G. F., A revision of the genus

Guazuma. Ceiba 1: 193 ff. 1951) offers data which very convincingly support the separation of *Herrania* from *Theobroma*.

A comparative study of the pollen of Herrania, Guazuma, Theobroma and other allied genera, outlined in detail below, has indicated that there are appreciable differences between the pollen of Herrania and Theobroma. There is still not complete agreement, however, in the generic interpretation of Herrania. In 1940, Ducke (Rodriguesia 4: 273. 1940) treated Herrania as a "subgenus (or section)" of Theobroma. A chromosome study of several species of Theobroma and Herrania carried out by Muñoz (Estudios cromosómicos en el género Theobroma L. Unpubl. Thesis. Fac. Inst. Interam. Ciénc. Agríc. Turrialba 30–35. 1948), indicates that the number in both concepts is 2n = 20. The chromosomes are very similar, but they are generally more slender and more definitely contrasted in Herrania albiflora, H. purpurea and H. pulcherrima (the only three species studied) than in those species of Theobroma which were examined. Muñoz

feels, but is not entirely certain, that *Herrania* should be treated as a section of *Theobroma*.

Most recently, Ducke (As espécies brasileiras do gênero *Theobroma* L. Bol. Técn. Instit. Agron. Norte 28: 3-20. 1953) has reiterated his belief that *Herrania* and *Theobroma* should be treated as a single genus. It is pertinent to this discussion that recently *Theobroma* and *Herrania* have been shown experimentally to be very closely allied. Ing. Agron. Addison, geneticist at the Instituto Agronômico do Norte in Belém do Pará, Brazil, successfully pollinated *Theobroma Cacao* with *Herrania Mariae*, but the embryos failed to develop (Addison, G. O'N., & R. M. Tavares, Observações sobre as espécies do gênero *Theobroma* que ocorrem na Amazônia. Bol. Técn. Instit. Agron. Norte 25: 1951).

Van Hall (Cacao. ed. 1. 1914; and ed. 2. 1932) treated *Herrania* as a section of *Theobroma*. On the other hand, Pound (Cacao and witchbroom disease (*Marasmius perniciosus*) of South America. 47 ff. 1938), while not definitely committing himself, outlined in very great detail the characteristics of *Herrania* and pointed out the important differences between *Herrania* and *Theobroma*.

The following key (adapted primarily from Schumann's key to his sections *Herrania* and *Eutheobroma* of the genus *Theobroma*) sets forth the gross characters by which *Herrania* may be separated from *Theobroma*.

A. Arbores parvae et graciles. Folia quinque- ad novem-digitata. Petalorum ligulae lineares vel filiformes, comparate longissimae, cucullum multo

SCHULTES, SYNOPSIS OF HERRANIA 227 1958]

superantes, in alabastro circinnato-involutae. Calyx usualiter 3-fidus. Fructus saepissimae conspicue costatus, pericarpio vulgo aliquid crassu-

AA. Arbores. Folia integra. Petalorum ligulae, duplo vel triplo cucullum superantes, vel breviores, in alabrastro reflexa vel erecta. Calyx usualiter 5-fidus. Fructus saepe obscure costatus vel sublaevis, pericarpio ut videtur saepius

Herrania Goudot, Ann. Sci. Nat. III. 2: 230. t. 5. 1844; Walpers, Rep. 5: 111. 1845-46; Endl. Gen. Pl. Suppl. 4: 62. 1850; Karst. Linnaea 28: 446. 1856; Tr. et Planch. Prodr. Fl. Novo-Granat. 209. 1862; Benth. et Hook. Gen. Pl. 1: 225. 1862; Walpers, Ann. Bot. Syst. 7: 225. 1862, 7: 430. 1868; Baill. Hist. Pl. 4: 131. 1873, Dict. Bot. 3: 49. 1891.

Lightia Schomb. Rep. Brit. Assoc. Adv. Sci. 2: 71. 1844. Non Lightia Schomb. Linnaea 20: 757. 1847. Brotobroma Karst. et Tr. ex Tr. Nuev. jén. y esp. plant. fl. Neo-Granad. 11. 1854.

TYPE SPECIES: Herrania albiflora Goudot.

GENERAL DISTRIBUTION: From Costa Rica down the Andes to Peru, along the Pacific coast of Colombia and Ecuador, across Venezuela and the Guianas and in the Amazonian basin of Brazil, Colombia, Peru and, probably, Bolivia.

ORIGINAL DESCRIPTION: Calyx 3-partitus, coloratus, deciduus, laciniis aequalibus concavis; aestivatio valvata. Corolla 5-petala, hypogyna, cucullato-concava, apice inflexo in ligulam linearem, ante anthesin concolutam, producta. Androphorum 5-fidum, carnosum, glabrum; laciniis sterilibus cum petalis alternantibus suprene in appendicem erectam vel reflexam dilatatis; laciniis fertilibus longitrorsum adnatis, petalis oppositis, brevioribus, singulis, 3-andris, antheris ovatis didymis. Stylus cylindraceus. Stigmata 5, teretiuscula, obtusa. Ovarium 5gonum, 5-loculare sessile, disco hypogyno destitutum. Ovula anatropa in singulo loculo anguloque centrali 1-seriata, horizontalia. Fructus ovato-oblongus, costatus, basi et apice subacuminatus, coriaceo-lignosus, indehiscens. Semina in pulpa nidulantia, ovata, angulata, testa pergamacea venosa. Embryo cotyledonibus crassis, hinc convexis, inde planis, radicula brevissima.

Small trees. Leaves unusually large, digitate, 4-9-foliolate. Flowers cauline, fasciculate. Calyx 3-5-fid; sepals more or less divided, valvate in the bud. Corolla 5-parted; petals hypogynous, cucullate-concave, apically inflexed, with a linear or filiform ligule which, before anthesis, is circinnate-involute. Androphore 5-fid, fleshy, glabrous; sterile segments alternate with the petals, enlarged above into erect or reflexed, ovatelanceolate or linear, petaloid staminodes; fertile segments 1-4 (mostly 3)-antheriferous, anthers short-stipitate, with diverging, didymous locules. Ovary sessile, 5-locular, the lower with many anatropous ovules. Style filiform, cylindrical. Stigmas 5, rather terete, obtuse. Fruit ovate-oblong, costate, apically usually subacuminate or acuminate, toughly coriaceous, JOURNAL OF THE ARNOLD ARBORETUM [vol. XXXIX indehiscent. Seeds enclosed in a pulp, flattened-ovate, angulate, with a papery testa, exalbuminous; cotyledons thick, sometimes flat, with a very short radicle. Chromosomes: 2n = 20 (in three species studied).

In his "Woods of northeastern Peru" (Field Mus. Nat. Hist. Bot. Ser. 15: 323–324. 1936), Llewelyn Williams has published what appears to be the only detailed description of the wood of *Herrania*. Williams cited five collections which were used as a basis for this description and referred all of the collections to "*Theobroma Mariae*." I have found that they represent *Herrania nitida*. Until wood samples are collected in exact correlation with herbarium specimens from many areas and for numerous species, an understanding of specific differences in the wood of *Herrania nitida* must serve as a guide to the wood structure of the whole genus.

Sapwood pale pink; heartwood pinkish brown. Wood has no distinctive odor or taste; straight- or wavy-grained, coarse-textured; light in weight and soft; requires a sharp knife to cut smoothly across grain; perishable. Growth rings absent or present. Parenchyma indistinct. Pores fairly small or very small; not numerous and well-scattered; solitary or in radial multiples of 2–3. Vessel lines fairly long, not prominent, but discernible to unaided eye. Rays coarse, lighter-colored than background, sometimes wavy, and conspicuous on cross section; darker than background and fairly distinct on tangential; of darker color than adjacent elements and conspicuous on radial surface. Pith light or dark greyish brown.

The examination of the pollen grains of *Herrania*, to the best of my knowledge the first which has been made, was carried out by Dr. Theodor van der Hammen of the Colombian Servicio Geológico Nacional. Pollen of *Herrania tomentella* was analyzed. All terms are used in accordance with Iverson and Troels-Smith's nomenclature proposed in 1950.

Herrania tomentella R. E. Schult. Pollen collection Serv. Geol. Nac. #IV 86. Collection Col. 34377.

Pollen grains: tricolporate, reticulate, subsphaeroidal; granulae of the muri visible but not separated. Lumina of reticulum irregular of size, rather large, polygonal, smaller near the colpae. In the lumina, rather faint granulae are visible. Colpae clear, edges separated; pores clear, without ectexine elements; sometimes indications of small transversal furrows. Magnitudo pollinis: media $(28-33 \ \mu)$. Magnitudo luminum: meso-macro $(2-4.7 \ \mu)$ and smaller. Index pollinis: subsphaeroidea (1-1.12); ('prolate sphaeroidal' of Erdtman). Index areae poli: middle (0.30-0.35). Index exinae: middle (0.05-0.08).

Van der Hammen reports further that *Theobroma*, *Guazuma*, *Sterculia* and *Herrania* have tricolporate and reticulate pollen grains but that the grains of *Waltheria* and *Helicteres* are of different types. A comparison of the four genera with tricolporate and reticulate grains leads to the really unexpected conclusion that, insofar as pollen morphology is concerned, there is no evidence that *Herrania* and *Theobroma* are very closely allied. On the contrary, the pollen grains of *Theobroma* resemble those of *Guazuma*

SCHULTES, SYNOPSIS OF HERRANIA 229 1958]

even more than they do those of Herrania. Van der Hammen compares the grains of Theobroma Cacao and of Herrania tomentella as follows: "The grains of Theobroma Cacao are subsphaeroidal ('oblate sphaeroidal' of Erdtman); index pollinis \pm 0.8–0.9; magnitudo pollinis \pm 22 μ . The polar area is relatively much larger than that of Herrania, the colpae are very narrow, unclear and short. Pores are small and not very clear; lumina of ret much smaller than those of Herrania (greatest size measured 1-1.75 μ), and more regular. Exine (including sculpture) relatively thicker than those of Herrania."

A most careful and detailed chemical analysis of the seeds of Herrania has been made by MacLean (MacLean, J. A. R., Oil-bearing seeds of possible economic importance to West Africa. Nature 169: 589. April 5, 1952). The material studied was reported to be referable to Herrania balaënsis and H. Mariae, but unfortunately no voucher specimens were cited for checking, and the specific identifications are open to doubt. The plants were introduced from Trinidad to West Africa in 1944. The photographs published on pages 589 and 590 would suggest that one of the species analyzed (probably the one called Herrania Mariae) was H. nitida. MacLean reported a very high oil content (up to 66.1%) of the seeds, and it is suggested that optimum cultural conditions might improve this figure. He found that the "percentage of total alkaloids is approximately one-third that of Amelonado beans, and the theobromine-caffeine ratio is reversed." The caffeine values were found to be comparable with the lower limit of range for coffee beans and kola nuts, with values greater than 1% being obtained on two occasions. Freshly extracted fat from Herrania seeds is liquid at 25-29°C with an odor resembling that of linseed oil; its specific gravity is 0.93-0.94; and its unsaponifiable matter is less than 1%. The figure for reducing sugars (0.4%) is four times that of Amelonado beans. The iodine values varied from 39 to 47, and the saponification value ran from 203 to 206. The percentage of free fatty acids in the oil ranged from 2.3 to 2.8 The composition of the oil was found to be 18-26% linoleic, 2-7% oleic and 74-76% of saturated acids.

Herrania comprises two groups of species which are sufficiently well marked one from the other to permit their segregation into sections. These two sections are not only distinct in the morphology of the flower; they also fall naturally into two distinct, though overlapping, geographical areas.

Sect. Herrania

Calyx patelliformis, sepalis media pro parte connatis. Subgeneris typus: Herrania albiflora Goudot.

Sect. Subcymbicalyx R. E. Schultes, sect. nov.

Calyx subcymbiformis, sepalis plerumque fere usque ad basim liberis. Subgeneris typus: Herrania nitida (Poepp.) R. E. Schultes. The characters upon which these concepts are founded serve for the

first dichotomy in the following key to the species. *Herrania albiflora*, *H. purpurea* and *H. umbratica* are the only species with the curious patelliform calyx. Their flowers, because of this condition, have a completely different appearance from those of all other species: the patelliform calyx lends a "closed" or compact appearance to the flower, whereas the subcymbiform condition allows for a greater expansion of the petals and their ligules and the staminodes. Furthermore, the ligules of *Herrania albiflora*, *H. purpurea* and *H. umbratica* are extremely short, whilst those of all other species are longer — with the single exception of *H. breviligulata*, very much longer.

The species of the section *Herrania* are confined to Middle America and the northernmost regions of Colombia in South America. Those of *Subcymbicalyx* extend over the whole northern half of South America, in northern Colombia overlapping the area occupied by the three species of Sect. *Herrania*.

Although, at the present state of our understanding of the genus, it is rather difficult to form any well founded phylogenetic picture, the patelliform calyx would appear to me to represent a derived condition and the subcymbiform calyx, conversely, a primitive condition in *Herrania*.

CLAVIS SPECIERUM HERRANIAE

- A. Calyx patelliformis. Sepala medio pro parte connata. Ligulae usque ad 20 mm. longae. Sect. HERRANIA.
 - B. Petala, ligulae et staminodia alba. Sepala usque ad 7 mm. longa.

 BB. Petala, ligulae et staminodia purpurea vel sanguinea.
 BB. Petala, ligulae et staminodia purpurea vel sanguinea.
 Sepala 12 mm. longa vel longiora.

- C. Ligulae usque ad 15 mm. longae. Capsulae costae valde inaequales, aliquid tenues, distantes. Fructus usque ad 9 cm. longus.
- CC. Ligulae 19 mm. longae vel longiores. Capsulae costae quasi aequales, crassissimae, non distantes. Fructus 11 cm. longus vel longior. 17. H. umbratica.
- AA. Calyx subcymbiformis. Sepala plerumque fere usque ad basim libera. Ligulae 25 mm. longae vel longiores. Sect. SUBCYMBICALYX.
 D. Foliola profunde incisa vel lobata.
 - E. Foliola grosse et regulariter pinnatisecta; lobulis anguste triangularilanceolatis, acutissimis; lamina subtus densissime et molliter stellatotomentosa, usque ad 60 cm. longa. Ligulae 180 mm. longae. Capsula maturitate fusco-rubescens; costis longitudinalibus bene conspicui et sine costis transversalibus prominentibus. 9. H. laciniifolia.
 EE. Foliola maxime grossissime sed irregulariter pinnatilobata; lobis late triangularibus, acutis lamina subtus aspera, stellatis cum pilis, usque ad 80 cm. longa. Ligulae 85 mm. longae. Capsula maturitate ochracea (?); costis transversalibus bene prominentibus.
 - DD. Foliola integra vel leviter dentato-sinuata vel undulata.
 - F. Ligulae 25-35 mm. longae. Foliola subtus cum indumento subcinereo-velutino. 3. H. breviligulata.

1958]

SCHULTES, SYNOPSIS OF HERRANIA 231

- FF. Ligulae 60 mm. longae vel longiores. Foliola subtus glabra vel cum indumento aspero vel molle, sed numquam velutino.G. Foliola glabra vel subtus sparsissime aspero-tomentulosa.12. H. nitida.
 - GG. Foliola variabiliter sed molliter pilosa vel tomentosa.
 - H. Foliola valde et regulariter sinuata.
 - I. Capsula costis quinque longitudinalibus rectis armata et laevis vel transverse striatofibrosa; maturitate flava. Staminodia quam 17 mm. longiora, apice acuta vel conspicue trifida.
 - J. Foliola maxima, 45-60 cm. longa vel saepissime longior
 - \times 19–35 cm. lata, latissime lanceolato-ovata, $\frac{1}{2}$ lata duplo longior quam latior, apicem versus grossiuscule sinuata, dentibus 5-9 cm. distantibus. Petala et ligulae rufo-purpurea. Ligulae 2-3 mm. latae. Staminodia JJ. Foliola minor, usque ad 60 cm. longa sed saepissime brevior \times 10–15 cm. lata, anguste lanceolato-elliptica, quadruplo longior quam latior, dentibus 2-4 (rarenter 5) cm. distantibus. Petala et ligulae albicantes. ligulae minores quam 2 mm. latae. Staminodia apice acuta. K. Foliola usque ad 30 cm. longa \times 11 cm. lata. Sepala inaequalia; majora 15-16 mm. \times 15 mm.; minora 10 mm. \times 6 mm. Petala 9 mm. \times 7 mm. Staminodia lanceolato-elliptica, 22 mm. \times 6 mm. KK. Foliola usque ad. 60 cm. longa sed vulgo brevior
 - × 15 cm. lata. Sepala subaequalia, 14 mm. Petala 8 mm. × 5 mm. Staminodia elliptica, 18 mm. × 8 mm. 2. H. balaënsis.
 II. Capsula costis quinque longitudinalibus rectis armata sed etiam transverse bene costata, in junctionibus costarum longitudinalium et transversalium projectionibus spiniformibus longis, mollibus et crassis productis; maturitate sanguinea vel rarenter flava. Staminodia usque ad 14 mm. longa, apice valde obtusa. 4. H. Camargoana.
 HH. Foliola normaliter integra, subintegra vel apicem versus plus minusve sinuosa.
 - L. Foliola lanceolato-oblonga, usque ad 60 cm. longa \times 22 cm. lata, basi longe et sensim attenuato-decurrentia. Petioli 45-60 cm. longi.
 - M. Capsulae costae tenues, late cultriformes, principaliter costa versus pilis urticantibus armatae, tactu asperae; capsula alibi glabra vel glabrescens.

MM. Capsulae costae crassae, hebetato-rotundatae, sine pilis urticantibus; capsula omnino molliter indumento stellato-velutino armata.
 N. Capsula ovoidea, apice breviter cuspidata vel subrotundata, costis minoribus, primariis usque ad 2 mm. altis, secundariis haud prominentibus.

NN. Capsula ellipsoidea, apice obtusa vel attenuata, costis majoribus, primariis usque ad 8 mm. altis, secundariis usque ad 3-5 mm. altis.

O. Capsula 10-12 cm. longa, 4-5 cm. in diametro, apice longe et sensim attenuata, cum costis hebetatis crassissimis, non bene distantibus, inter costas prominenter fibroso-rugosa. Ligulae usque ad 90-100 mm. longae. Staminodia apice leviter trifida. ... 13. H. nycterodendron. 00. Capsula 9 cm. longa, 4 cm. in diametro, apice vulgo obtusa, cum costis hebetatis crassis, bene distantibus, inter costas paullo et leviter fibrosorugosa. Ligulae usque ad 70 mm. longae. Staminodia apice acuta. 16. H. tomentella. LL. Foliola obovato-oblonga vel subrhomboidea, usque ad 31 cm. longa \times 12 cm. lata, basi aliquid attenuata vel quasi cuneata. Petioli plus minusve 30 cm. longi. P. Foliola obovato-oblonga, vulgo 35 cm. longa vel minora. Sepala aequalia vel subaequalia, 21 mm. longa \times 12 mm. lata, intus subdense ferrugineo-pilosa. Petala 11-12 mm. \times 5-6 mm. Ligulae atrosanguineae vel atropurpureae, 100 mm. longae, 2 mm. latae. Staminodia lanceolata, apice acutissima, integra 12–15 mm. \times 5 PP. Foliola rhomboideo-obovata, vulgo 30-35 cm. longa. Sepala valde inaequalia; majora 12–15 mm. longa \times 6–10 mm. lata; minora 11–13 mm. \times 11–12 mm., intus

glabra vel minutissime pilosa. Petala 7–9 mm. \times 6–8 mm. Ligulae albicantes, 75–100 mm. longae, usque ad 1 mm. latae. Staminodia lanceolato-elliptica, apice obtusa et saepe indentato-mucronata vel serrata, aliquid sinuato-undulata, 20 mm. \times 6–7 mm. 11. H. Mariae.

- Herrania albiflora Goudot, Ann. Sci. Nat. Paris III. 2: 230. t. 5, fig. 1-10. 1844; Tr. et Planch. Prodr. Fl. Novo-Granat. 1: 209. 1862; Schultes, Caldasia 2: 325. 1944.
 - Theobroma albiflorum (Goudot) De Wildeman, Pl. Trop. Grande Cult. 90. 1902.

DISTRIBUTION: Northern sector of the Magdalena basin in Colombia and in westernmost Venezuela.

Small tree up to 16 feet tall consisting of several round, simple or (rarely) branching trunks, 11–14 cm. in diameter, with a greyish bark. Leaves grouped at the apex of the trunk, digitate, stipulate, 5–6-foliolate. Branches densely and minutely ferruginous-tomentulous, probably becoming almost glabrous. Petioles terete, densely and minutely ferruginous-villose, somewhat dilated at the base, as long as the leaves, conspicuously striate-sulcate, up to 45 cm. long, 4–6 mm. in diameter. Stipules conspicu-

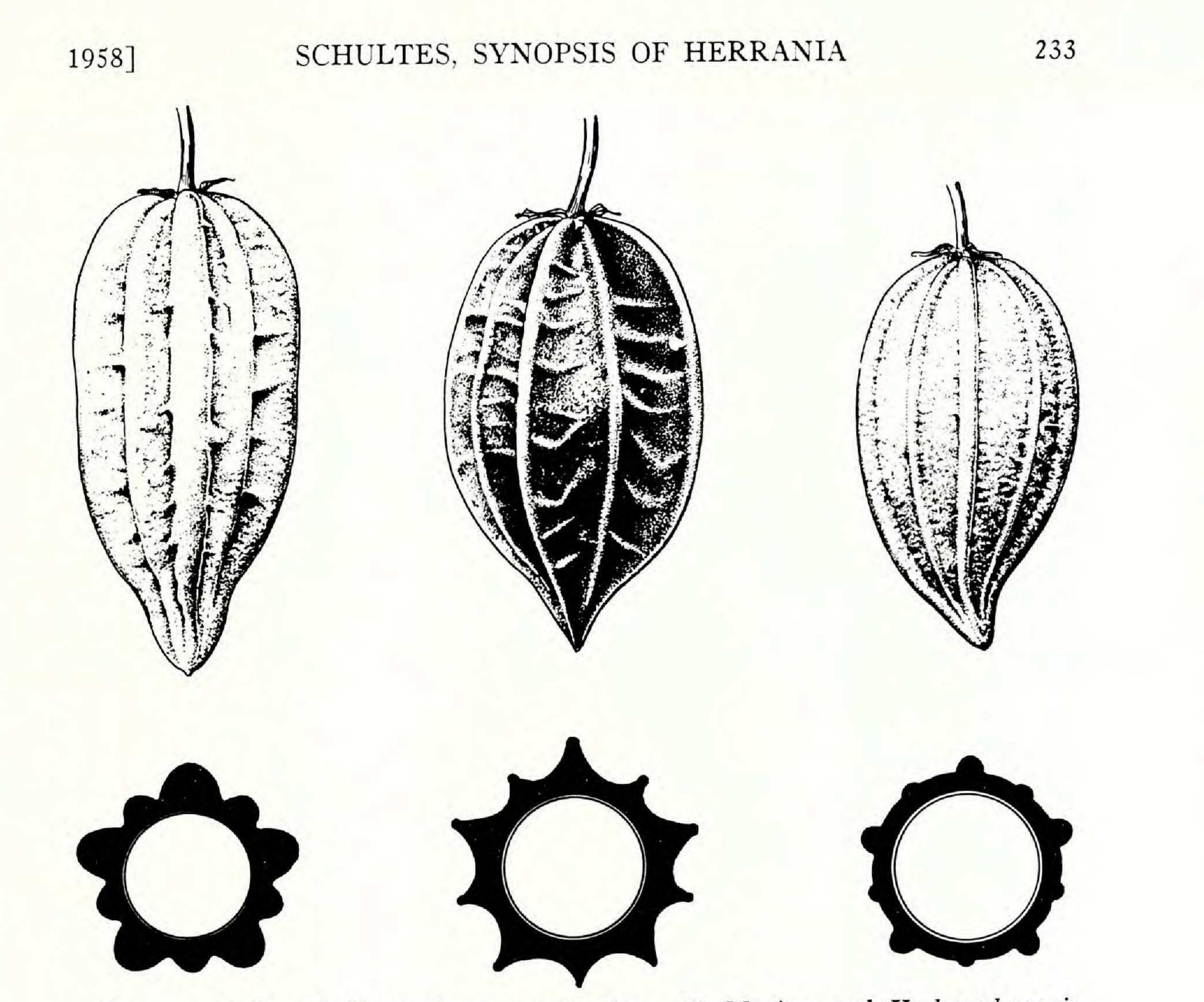


FIG. 1. Fruits of *Herrania nycterodendron*, *H. Mariae*, and *H. kanukuensis* (left to right) with schematic cross sections.

ous, linear, entire, acute, caducous, ferruginous, 50 mm. long, 3-4 mm. wide. Leaflets lanceolate-obovate, acuminate, basally long-attenuatedecurrent, very shortly petiolulate (petiolule strong, 3-4 mm. long), marginally entire, thin-chartaceous, 20-60 cm. (usually 50 cm.) long, 9-15 cm. wide, dark green and glabrous above, pale green and almost glabrous, or with extremely remote and microscopic stellate hairs, beneath; the veins of both surfaces prominent, clothed with ferruginous, minute and weak puberulence. Inflorescence fasciculate, few-flowered (5 or 6 flowers). Flowers subglobose, 15 mm. in diameter, borne in contracted racemes on the lower and middle part of the trunk, white, pedicellate. Pedicels very short, cylindric, fulvous-tomentulose, subtended at the base by a minute, very densely fulvous-tomentulose, linear bract. Flower buds small, globose, tomentose. Calyx patelliform. Sepals 3, subequal, connate half their length, rotund-ovate, rounded, marginally entire, yellowish white, externally densely stellate-villose, internally glabrous, about 7 mm. long, 6 mm. wide. Petals 5, very broadly rotund-ovate, cucullate, glabrous near the apex, thick-membranaceous, somewhat muricate-granulose on both surfaces, 5 mm. long, 4 mm. wide, longitudinally striate-veined, internally with conspicuous veins, ligulate, white. Ligules linear, reflexed, white, glabrous,

JOURNAL OF THE ARNOLD ARBORETUM 234 VOL. XXXIX membranaceous, with 6 or 7 brownish nerves, up to 2 cm. (usually shorter) long, less than 1 mm. wide at the base. Stamen tube 5-fid, alternately 2- and 3-antheriferous with short, simple, free filaments and 2-locular,

divergent, longitudinally dehiscent anthers. Staminodes petaloid, very broadly ovate, acute, reflexed, 6 mm. long, 5 mm. wide, densely muricategranulose on both sides, marginally entire. Pistil short, more or less 1.5 mm. long. Style linear, erect, glabrous with a 5-parted stigma. Ovary sessile, subglobose, pilose, 1.3 \times 1 mm. Fruits capsular, oblong, apically short-acuminate, the tip somewhat rounded, hispid, 10-costate, yellow when ripe, 11-14 cm. long. Seeds 30-40, irregular, compressed, enveloped in a white, mucilaginous pulp, slightly acid, covered with an internal membranous tegument and an internal pellicle, coriaceous and exteriorly rugose. Embryo brown, with 2 thick, unequal, rarely folded cotyledons and a very short radicle.

Colombia. [No definite locality, probably near Mariquita], Exped. Bot. Mutisii Novae-Granat. 3759. ANTIOQUIA: Vuelta de Acuña, Río Magdalena [leaves only referable to H. albiflora], Pennell 3799; opposite Boca Carare, alt. 125 m., Pennell 3832. BOLIVAR: Bojorque [Bohórquez], Río Magdalena, Bonpland 1580; Norosi-Tiquisio Trail, Lands of Loba, alt. 150-600 m., Curran 135; Boca Verde, Río Sinú, alt. 100-300 m., Pennell 4208. CUNDINAMARCA: Muzo, Goudot s.n. (Type); Río Guaco, near Muzo, Purdie s.n. SUR DE SANTANDER: vicinity of Puerto Berrio, between Carare and Magdalena Rivers, alt. 100-700 m., Haught 1598. Venezuela. ZULIA: vicinity of Perija, Tejera 268. Trinidad. Royal Botanic Gardens, Port-of-Spain, No Collector Cited; Bailey s.n.; Imperial College of Tropical Agriculture, Diego Martin Estate, Schultes 18639.

Herrania albiflora is very closely allied to H. purpurea from which it can be distinguished by its white or cream-colored flowers. There are also other differences: the sepals of Herrania albiflora are usually much smaller than those of H. purpurea; the stipules of the former are longer than those of the latter species; the leaflets of H. albiflora are lanceolate-obovate, whereas those of H. purpurea tend to be obovate-oblong; and the petals of the former species are very broadly rotund-ovate, 5 mm. \times 4 mm., whilst those of the latter are obovate, 8 mm. \times 8 mm.

The habit and general floral structure of Herrania albiflora, H. purpurea and H. umbratica are strikingly similar. These species alone in the genus have a patelliform calyx, which gives the flower a completely different appearance from the usual cymbiform calyx. The ligules in these three species are likewise similar in structure and are under 20 mm. in length. Purdie s. n., one of the earliest collections of the species, was identified as Herrania albiflora at Kew by Planchon, who annotated the sheet, a topotype. The report of the collector of this specimen relative to his having seen "several hundreds of fruits" on a cultivated tree of Herrania albiflora must be recognized as an exaggeration. Although fruits are often very numerous in most of the species of Herrania, I have never met any condition which would indicate "hundreds of fruits".

It has always been presumed that the type of Herrania albiflora, the

type-species of the genus, was preserved in the herbarium at Paris, but in June, 1950, I found Goudot material at Geneva which may very well be the type of Herrania albiflora. In Geneva, there are three sheets representing the Goudot collection of this species, all labelled, in his handwriting: "C. N. 1 Herrania albiflora mihi. Annales Sc. Nat. 1844. Muzo." One sheet has several very young and membranaceous leaves and an envelope in which there are fragments of a fruit belonging possibly to an annonaceous plant and which, by some error, have been associated with the Herrania collection. Another sheet has a complete and mature leaf. The third sheet has three envelopes: one contains several seeds of Herrania albiflora; another has a few flowers and a very young capsule; the third has a flower completely dissected, with the parts glued flat to the envelope. An examination of these floral parts and of Goudot's description and drawing of Herrania albiflora leads me to the conclusion that, at least for the flowers and fruits, the Geneva material is the type of the species and genus. As to how has it been possible for Goudot type material to find its way to Geneva one cannot be certain. There are, of course, many Goudot collections in the Delessert Herbarium (cf. A. Lasègue, Musée Botanique de M. Benjamin Delessert. 471. 1845). It may be of interest to note that a comparison of the Goudot floral dissection with the description of Herrania albiflora has uncovered several minor discrepancies or omissions. The sepals, described as glabrous within, have a very minute and sparse puberulence on the lower portion of the inner surface; and the petals are extremely muricate-granulose externally, as are also the very short ligules in the basal portion near their junction with the petal. One of the Mutis plates in Madrid, executed by the Colombian botanical artist Francisco Javier Matíz, represents a fruiting and flowering branch of Herrania albiflora. Not only are ripe and unripe fruits shown in excellent detail, but a large number of flowers are depicted so painstakingly that it is clear that Mutis and his colleagues could, so long ago, differentiate between the patelliform calyx of Herrania albiflora and the subcymbiform calyx of the other species illustrated. No foliage is drawn on the plate of Herrania albiflora. Triana correctly annotated this plate as "Herrania albiflora Goudot." In the Mutis collection of plants in Madrid, there is a sterile collection of leaves, misidentified as "Theobroma Mariae," which represent Herrania albiflora. They undoubtedly belong to the plant the flowers and fruits of which are portrayed on the Mutis plate of Herrania albiflora. Van Hall (Cacao. ed. 2. 74. 1932) claims that "according to Goudot, who collected this species near Muzo (Colombia), the seeds are mixed with those of the commercial cacao for home use; they are said to improve the taste of the chocolate." He credits Goudot with the report that "the seeds are also used, unmixed, for the preparation of a very bitter product which is used by the population as a febrifuge". Herrania albiflora is generally recognized as a cacao-relative. Hart (Cacao. 13. 1911) reports that "Herrania albiflora and Pachira insignis

JOURNAL OF THE ARNOLD ARBORETUM 236 VOL. XXXIX have both been sent to the author as 'wild' cacao, but neither of these trees has anything in common with Theobroma Cacao and neither of them produces saleable samples".

1a. Herrania albiflora Goudot f. titanica R. E. Schultes, Caldasia 3(15): 442. t. pag. 443. 1945.

DISTRIBUTION: Western or Magdalena slope of the eastern Cordillera in the Departamento del Sur de Santander, Colombia.

Usually a robust tree up to 30 feet in height, differing from Herrania albiflora principally in having much larger leaves and flowers.

Colombia. SUR DE SANTANDER: Carare, Landazuri alt. 1000 m., Richter s.n. (Type); vicinity of Barranca Bermeja, Magdalena Valley, between Sogamosa and Colorado Rivers, alt. 100-150 m., Haught 1490.

The collection L. Richter s. n. seems to present clear evidence that there exists a very large variant of Herrania albiflora, which may probably best be treated as a distinct forma. The leaves are not only very large for the species, but, in Richter s. n., the entire plant is exceptionally robust for the genus, measuring up to 10 meters in height. The height of the plant from which Haught 1490 came is not given, but the collector notes that it was "a small tree;" this would seem to indicate, in the case of such a meticulous collector as Haught, that it was not, as in nearly all the species known, a "treelet." The leaves of Haught 1490 are much larger than in

the Richter collection.

I have found that within a species of Herrania the size of the leaves is more or less standard, regardless of whether it grows in shaded forest or open pasture. This causes me to feel that the unusual size of the leaves of Herrania albiflora f. titanica does not represent a mere ecological variant. Vegatatively, the new form is almost indistinguishable from Herrania umbratica of the same general region, but there are important differences in the fruits (Caldasia 2: 261-264. tt. 2, b, c, d. 1943). It is unfortunate that, except for the drawing which accompanies the original description, we know very little of the fruit of Herrania albiflora. The capsule of Herrania albiflora f. titanica is similar to that of H. purpurea, being somewhat intermediate between H. purpurea and H. umbratica. It measures 12.5-14 cm. in length and 5-5.5 cm. in diameter and has low, rounded unequal ribs; the apex is acuminate.

Richter informed me that he collected a few dried flowers from the base of the type of Herrania albiflora f. titanica and that they showed evidence of having been white or yellowish in life. Unfortunately, these were lost in shipment. The color of the flower in Haught 1490 is uncertain, for the label bears no note in this respect. But with Haught 1598 (a collection representing Herrania albiflora) is a note stating: "a small cauliflorous tree, cf. 1490, from which this differs in having white flowers."

2. Herrania balaënsis Preuss, Exped. Centr.- und Süd-Amerika (1899-

1901). 253. t. 7. 1901; Bull. Soc. Études Col. Ann. 9(4): 220. t. pag. 221. 256, fig. 1-8. 1902 (non accurate titulata).

Theobroma balaënsis (Preuss) De Wildeman,² Pl. Trop. Grande Cult. 89. 1902.

Small tree up to 25 feet in height, with a slender, simple, very straight cylindrical trunk about 15 cm. in diameter at the base. Leaves arranged at the apex of the trunk, digitate, usually 7-foliolate, petiolate. Petioles terete, sulcate, very densely ferruginous-tomentose, up to 30 cm. long, about 5 mm. in diameter. Leaflets unequal, lanceolate-elliptic, marginally conspicuously sinuate, apically strongly acuminate, basally long attenuatedecurrent, sessile, firmly chartaceous, up to 60 cm. long, 15 cm. wide; leaf blade dark green and glabrous or subglabrous (microscopically scabridulous with minute stellate puberulence) above, brownish green and very densely and softly ferruginous-stellate-pilose beneath; the veins prominent and brown-tomentose on both sides, especially beneath. Inflorescence fasciculate, many-flowered (12-15 flowers), on the lower and middle portions of the trunk. Pedicels robust, densely greyish stellate-pilose, 8-9 mm. long, 1-1.5 mm. in diameter, subtended at the base by a minute, very densely stellate-pilose, linear bract. Calyx subcymbiform. Sepals 3, subequal, externally reddish brown, internally deep purple, lanceolate-elliptic, apically subacute, marginally entire, very densely muricate-papillose or granulose, 14 mm. long, 6 mm. wide. Petals 5, very broadly ovate, strongly cucullate, 8 mm. long, 5 mm. wide, whitish with 8-10 purplish veins, densely muricate-papillose, sparsely stellate-pilosiusculous externally, papillose, glabrous internally, ligulate. Ligules of the petals white and rose-colored, filiform, glabrous, very minutely granulose, membranaceous, 100 mm. long, less than 2 mm. wide. Staminal tube 5-parted; stamens alternately 2- and 3-antheriferous with relatively long, simple, glabrous filaments and 2-locular, divergent, longitudinally dehiscent anthers. Staminodes 5, petaloid, reflexed, membranaceous, elliptic, apically acute, marginally entire, glabrous, minutely and densely muricate-granulose on both sides, probably purplish red, 17-18 mm. long, 7-8 mm. wide. Pistil about 5 mm. long. Style linear, erect, glabrous with a 5-parted stigma. Ovary sessile, subglobose, 5-ribbed, densely white-pilose, 1.8-2 mm. in diameter, 3 mm. long. Fruit elongate-ovoid, the apex long-acuminate, 10costate with 5 primary and 5 secondary ribs, olive-green when young, yellow-green and hispid when ripe, about 14 cm. long.

Ecuador. Río de Peripa, Andre K26; El Recreo, Eggers 14362; Balao, Eggers 14362. Trinidad. CULTIVATED: Imperial College of Tropical Agriculture, Diego

Martin Estate, Schultes 18638.

Herrania balaënsis appears to be most closely allied to H. kofanorum. This relationship will be discussed under Herrania kofanorum. This species also resembles H. Dugandii, from which it differs in being very

² This combination, as "Theobroma balonsis," has recently been made by Llano Gómez (p. 18, Cultivo del cacao. Publ. Min. Econ. Nac. Bogotá. 1947), who apparently was unaware of the earlier publication.

much larger in its vegetative parts; in having conspicuously sinuate (instead of nearly entire) leaflets; in having much smaller sepals which are externally granulose (instead of stellate-pilose) and smaller petals which are whitish (instead of red-purple) and sparsely covered with a stellate puberulence; in having much larger staminodes; and in several other minor respects.

Herrania balaënsis has a type of fruit which immediately sets it apart from most other species. The structure of the fruit, according to the drawing of the capsule which was published with the original description, is

similar to that of an unrelated species, Herrania kanukuensis.

The specific epithet *balaënsis* refers to the locality from which the type was taken.

Llano Gómez (loc. cit. 18) reported that this species is cultivated to some extent in Ecuador, but whether this refers to the toleration of the plant as a wild intruder in plantings or to actual cultivation is not clear. It seems probable that *Herrania balaënsis* is actively cultivated.

3. Herrania breviligulata R. E. Schultes, Caldasia 1: 19-24. t. pag. 21, figs. 1-4, t. pag. 24, fig. 5. 1942.

DISTRIBUTION: Upper reaches of the Putumayo River, Colombia, and adjacent Ecuador.

Small, slender, graceful tree up to about 15 feet in height. Trunk erect, branching near the apex, terete, 6–7 cm. in diameter, with ashy-brown

rimose-scrobiculate bark. Branches apparently tomentose, becoming glabrous. Branchlets densely villose, with rust-colored hairs, becoming almost glabrous. Leaves large, 4- or 5-digitate, very long-petiolate. Petioles terete, basally slightly swollen, subferruginous, tomentulose, up to 46 cm. long, about 0.5 cm. in diameter. Leaflets sessile, unequal, lanceolate-oblong, the margin entire, firmly chartaceous or papyraceous, mostly 20-40 cm. long, 6-30 cm. wide, very cuspidate-acute, up to 3 cm. long-decurrentattenuate, puberulent on both surfaces but especially so beneath; above light green, very sparsely and minutely stellate-pubescent with white hairs, beneath pale green, densely and velvety stellate-villose-sericeous; the veins prominently elevated and brown-tomentose on both surfaces but especially so beneath. Inflorescence fasciculate, 5-8-flowered. Flowers cauline, in contracted racemes from the upper portion of the trunk, dark crimsonpurple, pedicellate. Pedicels about 5-7 cm. long, very densely browntomentose, articulate, basally subtended by a short, linear, very densely brown-tomentose bract 1-1.5 mm. long. Bud globose, 4-9 mm. in diameter, very densely rusty-villose. Calyx 3-parted, divided almost to the base, subcymbiform. Sepals 3, broadly elliptic-oblong, obtuse, marginally slightly revolute, crimson-purple, 13-14 mm. long, 7-9 mm. wide, internally very sparsely puberulent or glabrescent, externally beset rather densely with long, white, stellate hairs, valvate in the bud. Petals 4, basally sessile, obovate, 6-7 mm. long, 5-6 mm. wide, concave, strongly cucullate, muricate-papillose or granulose on both surfaces but especially so externally,

SCHULTES, SYNOPSIS OF HERRANIA 1958] 239

5-nerved, longitudinally striate-veined, internally with prominent veins, dark crimson-purple, ligulate. Ligules linear, 25-35 mm. long, 1.5-2 mm. wide, hanging, basally slightly and abruptly contracted, apically slightly inrolled in a spiral position, 3-nerved, yellowish-red, with purple nerves, very minutely muricate-papillose or granulose. Staminal tube 5-parted, with stamens alternately 2- and 3-antheriferous and simple, short, free filaments. Staminodes petaloid, dark scarlet, lanceolate-elliptic, acute, margin entire, muricate-granulose on both surfaces, 15 mm. long, 4 mm. wide, crimson-purple. Pistil 2.8 mm. long. Style terete, simple, purplish, with a deeply 5-parted stigma. Ovary sessile, very densely pilose, pale yellow, subglobose, 3 mm. long, 2 mm. wide. Fruit unknown, but said to be pale yellow when ripe.

Colombia. PUTUMAYO: Mocoa, alt. 850 m., Schultes & Smith 2050 (Type), Schultes & Cabrera 19082, Anglo-Colombian Cacao Collecting Expedition (Cope & Holliday) 78; Río Caquetá, Puerto Limón, Schultes & Cabrera 18720. Ecuador. NAPO-PASTAZA: near Archidona, alt. 650 m., Mexia 7320.

Herrania breviligulata seems to be closely allied to no other known species of the genus. In some respects it resembles H. Cuatrecasana but can be separated from this species readily by having seven (instead of four or five) smaller leaflets with an entire (instead of crenate-denticulate) margin, a more cuneate base and a much softer and denser indumentum on the lower surface; an inflorescence with only six or eight (instead of eighty or ninety) flowers; much smaller buds; pedicels which are 5-7 mm. (instead of 20-30 mm.) long; somewhat smaller sepals and petals; ligules 25-30 mm. (instead of 130 mm.) long; and much smaller staminodes (14 mm. \times 4 mm. instead of 25 mm. \times 8 mm.) which are apically acute. Both species are known only from the upper reaches of the Putumayo River and adjacent regions, an area which would appear to be one focus of speciation in the genus.

Herrania breviligulata has the shortest ligules known for any of the species with a subcymbiform calyx, a characteristic which is suggested by the specific epithet. It is likewise distinguished from all other known species by the very soft and dense, greyish indumentum which is velvety on the under surface of the leaflets.

The Ecuadorean collection Mexía 7328 bears the data: "Fruit green, deeply ribbed." I have been able to find only one specimen of this collection (that in the Riksmuseum in Stockholm) and this is without a capsule. The fruit of Herrania breviligulata, therefore, remains unknown, Mexía's field notes notwithstanding.

- 4. Herrania Camargoana R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. 14: 120. tt. 29, 32. 1950.
 - Theobroma Camargoana (R. E. Schultes) Ducke, Bol. Técn. Inst. Agron. Norte 28: 15. 1953.
 - DISTRIBUTION: Upper Rio Negro basin in Brazil and Colombia.

Small, slender and graceful tree, usually up to 10 (but sometimes up to 27) feet tall. Trunk erect, sparsely branched or else unbranched near the top, about 4-5 inches in diameter, covered with a black bark. Branches tomentose, but soon glabrous. Branchlets densely villose, ferruginous, subglabrescent. Leaves very large, digitate, 7- to 9-foliolate, very longpetiolate. Petioles terete, strongly constricted at the base, softly goldenferruginous-tomentellous, up to 60 cm. long, 10 mm. in diameter. Stipules persistent, subulate, very densely tomentellous, up to 3 cm. long. Leaflets sessile, oblanceolate or broadly lanceolate-ovate, slightly erect, unequal, membranaceous-papyraceous, acuminate, basally attenuate, marginally regularly and conspicuously sinuate in the upper half and everywhere armed with cilia-like stellate hairs (up to 1.5 mm. long), 60-75 cm. long, 16-26 cm. wide, asperous above, sparsely pilose with long and single hairs, beneath rather softly tomentellose with long stellate hairs. Inflorescence fasciculate, many-flowered, growing from all parts of the trunk but principally from the lower portions. Pedicels articulate, up to 28 mm. long, 0.8 mm. in diameter. Buds globose, up to 10 mm. in diameter, stellate-pilose. Calyx 3-parted, divided nearly to the base, subcymbiform. Sepals widely elliptic-oblong, subacute, marginally entire, externally dark purple, internally blood-red, mostly 12 mm. long, 8–9 mm. wide, glabrous within, stellate-pilose with rust-colored hairs (up to 1 mm. long) and very minute white hairs without. Petals 5, sessile, obovaterotund, very strongly concave-cucullate, about 8 mm. long, 6 mm. wide, with 5 dark purple longitudinal nerves as well as finely reticulate nerves, elsewhere yellow, externally conspicuously muricate-verrucose, apically extended into a ligule. Ligules linear, mostly 90 mm. long, at the base 1.7 mm. wide, apically filiform, at the very base blood-red but for the greater part of their length whitish yellow. Staminal tube 5-parted with 2-antheriferous stamens and short free and simple filaments. Ovary ellipsoid, 3.5 mm. long, 2-2.5 mm. in diameter, very densely and coarsely white-pilose. Style terete, simple, yellow, with the stigma apically inconspicuously 5parted, 3 mm. long. Staminodes conspicuous, rhomboid-elliptic, obtuse, marginally entire, verrucose on both surfaces, ashy purple, 14 mm. long, 5 mm. wide. Fruits numerous, almost globose, or slightly ellipsoid, apically very abruptly long-apiculate (apicule 2-2.5 cm. long), mostly 8-8.5 cm. long, 3.5–4.5 cm. in diameter, basally attenuate, with persistent sepals, longitudinally 10-costate with the primary and secondary ribs almost equal, thin, knife-shaped, irregular in height but for the most part (in life) 5-6 mm. high, transversely irregularly but conspicuously costate with knifeshaped ribs, which are slightly lower or often somewhat higher than the longitudinal ribs, the junction of the longitudinal and transverse ribs prolonged into a softly carnose, mammose or spine-like projection (which is somewhat blunt at the tip) with stinging, stellate hairs in all parts but especially along the ribs; the pericarp thick, usually dark red or blood-red (but sometimes yellow) when ripe; seeds 25, obtusely round-pyramidal, about 9 mm. long \times 11 mm. wide \times 7 mm. thick, imbedded in a white pulp.

241

Brazil. AMAZONAS: Rio Negro, Serra de São Gabriel, Schultes & López 9722 (Type); Rio Negro, Fróes 21468; Rio Negro, Uaupés (São Gabriel), Fróes 21540; summit of Serra de São Gabriel, alt. 100 m., Schultes & López 8758, 8759, 8762, 8763, 9162, 9619; Tapurucuara (Santa Isabel), Schultes & López 8956; Serra de Uanarí, Murça Pires 775; Schultes & Murça Pires 8978; mouth of Rio Xié, Schultes & López 9205; Nazaré, Schultes & López 9240; Serra Jacamín, Schultes 9747; between São Felipe and Karapaná, Schultes & López 9869; Rio Padauiary, Fróes 22673; Rio Uaupés, between Ipanoré and confluence with Rio Negro, Serra Wabeesee, on left bank below Bela Vista, Schultes & López 9144 (Type of flowers); Schultes & Murça Pires 9130; Murça Pires

1159.

Colombia. VAUPES: Caño near north end of Inambú, Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 56; Río Negro, San Felipe and vicinity (below confluence of Río Guainía with Casiquiare), alt. about 600 ft., Caño Marijabo, Schultes, Baker & Cabrera 18050; Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 45.

Restricted apparently to the uppermost Río Negro basin of Brazil and Colombia, Herrania Camargoana seems to have as its closest ally the Guianan and Venezuelan H. lemniscata. This relationship is strikingly evident when one compares the fruits of the two concepts. Both species have relatively small capsules in which there are transverse ribs nearly as large as the cultriform longitudinal ribs, and soft, pointed mammoid projections at each junction of the longitudinal and transverse ribs. The former species, however, has much longer and more upturned projections than the latter, and would seem, in this as in some other characters, to represent an extreme in the evolution of the genus. There would appear to be a rather easily traceable trend from Herrania Mariae through H. lemniscata to H. Camargoana, on the one hand, and to H. laciniifolia on the other. The coloration of the flowers of Herrania Camargoana and H. lemniscata is similarly complex and may also indicate a relationship. No other known species of Herrania can match these two for complexity of floral coloration. Herrania Camargoana has sepals which are dark blood-red externally but scarlet internally; petals which are ashy red or purple with yellowish stripes; staminodes which are ashy purple-maroon with white-yellow patches internally but entirely dark red externally; and ligules, red without and white-yellow within, which are folded or inrolled, so that the red is enclosed and is not seen directly. Herrania lemniscata has, according to field notes (Steyermark 60558), sepals which are white in the uppermost two-thirds and rose-salmon below, with rose stripes; and staminodes (called "petals" on the label) which are dull yellow with dull rose specks in the lower half. The shape and size of the leaflets, however, differ strikingly in the two concepts. Herrania Camargoana has oblanceolate or broadly lanceolateovate leaflets which measure 60–75 cm. in length and 16–26 cm. in width with the upper half regularly and conspicuously sinuate. Herrania lemniscata has leaflets which are at least 80 cm. long and 40 cm. wide with the margin very deeply pinnatilobate with usually four irregular and, for





FIG. 2. Crown of Herrania Camargoana.

the most part, widely triangular or widely lanceolate-acuminate segments, each up to 18 cm. long and 9–10 cm. wide.

Herrania Camargoana is unusually abundant near the summits of the isolated granitic mountains of the upper Río Negro valley. It has also been found in sandy patches along the banks of the rivers themselves. A search through the Spruce collections and notes from this area has failed to turn up any evidence of Herrania Camargoana in the extensive material which this early explorer gathered in the long period (1851–1856) which he spent in diligent study of the area to which the species is confined. There has been no collection of Herrania Camargoana made as yet from Venezuela, but it is undoubtedly represented in the upper Río Negro drainage area of that country.

Herrania Camargoana was named in honor of Dr. Felisberto Camargo, founder and first director of the Instituto Agronômico do Norte in Belém do Pará, Brazil.

5. Herrania Cuatrecasana García-Barriga, Caldasia 2: 57. t. 2. 1941. DISTRIBUTION: Upper reaches of the Putumayo River in Colombia.

Small tree 9 feet tall with whitish, maculate bark. Petioles terete, densely brown-stellate-tomentose. Leaves digitate, large, long-petiolate, 7-foliolate. Leaflets sessile, spreading, oblanceolate-oblong, the margins very remotely and obscurely crenate-denticulate, acuminate, basally long and gradually attenuate-decurrent, the lower leaflets about 33 cm. long, 9 cm. wide, the middle 50 cm. long, 17 cm. wide; the leaf surface papyraceous, above sparsely and minutely stellate-pubescent, the veins browntomentose, beneath softly stellate-pilose, the veins more prominent and hirsute above than beneath. Inflorescence fasciculate, 80-90-flowered. Flowers cauline, growing from the upper portions of the trunk, pedicellate. Pedicels slender, articulate, stellate-tomentulose, 2-3 cm. long, basally subtended by a linear or filiform, pilose, caducous bract. Buds ellipsoid or globose, 8-9 mm. in diameter. Sepals 3, equal, oblong, obtuse, dark purplish red, outwardly stellate-pilose with long hairs, inwardly with very short, reddish hairs, 15-18 mm. long, 7-11 mm. wide. Petals concave, rotund-ovate, strongly cucullate, glabrous, muricate-papillose, longitudinally striate-nerved, 10-11 mm. long, 7-8 mm. wide, with a long, filiform ligule, 130 mm. long, 1.5 mm. wide. Staminal tube 5-parted, with the stamens all bearing 4 anthers. Staminodes petaloid, purple, rhomboid-lanceolate, attenuate towards the apex, rather obtuse or acute, 25 mm. long, 8 mm. wide. Ovary shortly depressed, ovoid, densely pilose with whitish yellow hairs, 2 mm. long. Stigmas 3. Fruit ellipsoid, about 11-12 cm. long and 7-8 cm. in diameter, apically attenuate-acuminate, 10-costate, with 5 primary and 5 secondary ribs, cultriform, covered, especially along the ribs, with very minute stinging, stellate hairs, rind very thin and brittle, yellow when ripe. Seeds about 60, regular, compressed, triangular in outline, 14 mm. long, 12 mm. wide, 5 mm. thick, enveloped in a white, mucilaginous pulp, covered with a coriaceous tegument, exteriorly rugose.

Colombia. PUTUMAYO: Río Guamués, San Antonio de Guamués, alt. about 310 m., Cuatrecasas 11168 (Type); Río Uchupayaco, alt. 300 m., Schultes 3342; Mocoa and vicinity, alt. 1800–2400 ft., Schultes & Cabrera 19100; Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 80; Río Caquetá, Puerto Limón, Schultes & Cabrera 18712, 18715; Río Putumayo, Puerto Ospina and vicinity, Schultes & Cabrera 18976; Montclar, Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 86.

Ecuador. Río Sucumbios, 17 hrs. by motor upstream from Puerto Ospina. Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 84.

Apparently the closest ally of Herrania Cuatrecasana is H. tomentella. This relationship is discussed under Herrania tomentella.

Herrania Cuatrecasana has been considered to be related to H. Mariae through the concept H. Mariae var. putumayonis. It differs from H. Mariae chiefly in having leaflets which are very much more long-attenuate-decurrent at the base, in the indument and size of the leaflets, in the length of the pedicels, in having obtuse instead of acute sepals, and in having

very characteristic and conspicuous rhomboid-lanceolate staminodes, and in the length of the petals. It is much more softly and densely pubescent than *Herrania Mariae*. It is also apparently a very much smaller and weaker plant than *H. Mariae*.

244

Herrania Cuatrescasana likewise resembles H. Dugandii in some respects. The former differs from the latter principally in having denticulate, instead of almost entire, leaf margins and in being puberulent on both surfaces of the leaflets instead of being glabrous above. Furthermore, Herrania Cuatrecasana has many-flowered (80–90) inflorescences, whereas H. Dugandii has an inflorescence composed of but twenty flowers or fewer. The pedicels of the flowers of the former species are twice as long as those of the latter, and there are important differences in the shapes and sizes of the floral parts and leaflets.

Vegetatively, Herrania Cuatrecasana bears some resemblance to H. nycterodendron; this will be discussed under that species.

The description of the fruit of *Herrania Cuatrecasana* is based upon *Schultes 3342* from the Putumayo. The leaves and dried remains of floral parts adhering to the ripening fruits as well as floral parts which were collected on the ground at the base of the tree have enabled me to determine the specimens as representing the species in question.

The specific epithet *Cuatrecasana* honors the botanist Dr. José Cuatrecasas, formerly of the Instituto de Ciéncias Naturales in Bogotá, and the Chicago Natural History Museum, now at the Smithsonian Institution.

6. Herrania Dugandii García-Barriga, Caldasia 2: 59, 61. t. 3. 1941. DISTRIBUTION: Westernmost Amazonia, especially in the Putumayo basin of Colombia.

Small tree, 9 feet tall, sparsely branched at the apex of the trunk. Petioles terete, densely hirsute with reddish stellate hairs, 30 cm. long. Leaves digitate, long-petiolate, 7-foliolate. Leaflets sessile and spreading, the margins almost entire or near the apex slightly sinuate, obovate-oblong, acute or obtusely subacuminate, basally gradually attenuate, the lower 18 cm. long, 6 cm. wide, the middle 31 cm. long, 12 cm. wide; leaf surface firmly papyraceous or thinly coriaceous, above glabrous or very remotely strigillose, the nerves subimpressed and pubescent, beneath stellate-hirsute, roughish, the nerves reddish hirsute. Inflorescence axillary, 15-20-flowered. Flowers cauline in contracted, subumbelliform racemes, on the upper portions of the trunk, dark purple, pedicellate. Pedicels very densely browntomentose, articulate, 1 cm. long or shorter, basally subtended by a short linear, villous, caducous bract. Bud ovoid-oblong, 11 mm. in diameter, 18 mm. long. Calyx subcymbiform. Sepals 3, oblong, obtuse, dark purple, externally subdensely armed with stellate hairs, internally with very short rust-red hairs, up to 21 mm. long and 12 mm. wide. Petals concave, obovate, basally slightly attenuate, striate-nerved, glabrous, 11-12 mm. long, 5-6 mm. wide, apically strongly cucullate, with a long ligule. Ligule filiform, dark purple, 100 mm. long, 2 mm. wide. Staminal tube

5-parted. Staminodes narrowly lanceolate, basally and apically attenuate, apically very acute, squamulate-rugulose on both surfaces, 12–15 mm. long, 5 mm. wide. Ovary 4 mm. long, 3 mm. in diameter, densely covered with yellow hairs. Stigmas 5. Fruit unknown.

Colombia. Ритимачо: Río Putumayo, Puerto Porvenir, above Puerto Ospina near La Loma, alt. 230–250 m., *Cuatrecasas 10742* (Туре). Амаzonas: Trapecio Amazónico, Río Loretoyacu, alt. about 100 m., *Schultes 6038*.

Herrania Dugandii seems to be most closely allied to H. kofanorum, a

species from the same general region. Both are rather similar in their vegetative parts, although the leaflets and certain floral parts of the latter are very much larger than those of the former. Herrania kofanorum further differs from H. Dugandii in having much more coriaceous leaflets which are more deeply and regularly undulate-sinuate; in having very strongly unequal sepals, the outer one of which is apically slit (the sepals of Herrania Dugandii appear at once to be much longer than H. kofanorum because they are much narrower in relation to their length; but, in reality, they are smaller); in having round-ovate petals which measure 9 mm. \times 7 mm. (instead of obovate, basally attenuate petals measuring 11–12 mm. \times 5-6 mm.); in having a more filiform ligule which measures 80-100 mm. in length \times 1 mm. (instead of 100 mm. \times 2 mm.); and in having much larger staminodes, which measure 22 mm. \times 6 mm. (instead of about 12–15 mm. \times 5 mm.). These size differences combine with slight differences in shape of floral parts to give the flowers of the two species rather dissimilar aspects. It is obvious, however, that the two are closely related. Further collections and studies, especially when the fruit of both are known, may indicate that Herrania kofanorum should be treated as a variety of H. Dugandii.

The specific epithet *Dugandii* honors Dr. Armando Dugand, outstanding botanist, and director from 1940 to 1952 of the Instituto de Ciéncias Naturales of the Universidad Nacional, Bogotá, Colombia.

7. Herrania kanukuensis R. E. Schultes, Caldasia 2: 11. 1943; Bot. Mus. Leafl. Harvard Univ. 13: 277. 1949; ibid. 14: t. 33. 1950.

Theobroma Mariae (Mart.) Decaisne ex Goudot var. lobata Pulle, Rec. Trav. Bot. Néerl. 9: 151, 1912.

DISTRIBUTION: Southern Venezuela, adjacent Brazil and British and Dutch Guiana.

Small tree, slender and graceful, up to 16 feet in height. Trunk with a somewhat striate, brownish-black bark. Branchlets very densely browntomentose. Leaves large, 5- or 6- digitate, stipulate, very long-petiolate. Stipules caducous, linear, acute, somewhat rigid and dry, very densely brown-tomentose, 15 mm. long, basally about 1.5 mm. wide. Petiole strong, up to about 53 cm. long, 6–7 mm. in diameter, very densely and softly brown-tomentose, basally rather swollen, then abruptly constricted. Leaflets sessile, unequal, strongly obovate, abruptly acuminate, basally

abruptly cuneate, almost entire, often near the apex subundulate-sinuate and often very conspicuously, though minutely, mucronate (with the prolongations of the lateral veins up to 1 mm. long), firmly papyraceous, the central leaflets 30-44 cm. long, 13-16 cm. wide, above dark green or exceedingly sparsely hirsute, aspero-strigose with long white hairs noticeable along the veins, the veins very densely and softly stellate-pilose and rust-colored, the nerves on both surfaces, but especially beneath, prominently raised. Inflorescence fasciculate. Flowers not completely known (remains of the persistent calyx showing 3 densely brown-stellate-tomentose, elliptic-lanceolate, acute sepals, 14 mm. long, 6 mm. wide; the 5 petals, concave, strongly cucullate, elongate-obovate, about 8 mm. long, 4-5 mm. wide, ligulate). Fruit long-pedunculate (peduncle rather robust, densely stellate-puberulent, up to 3 cm. long, about 2-3 mm. in diameter), ovoid, 7-8 cm. long, about 4 cm. in diameter, apically very shortly cuspidate or subrotundate, basally rounded, extremely velutinous with dense and minute stellate-puberulence, lacking stinging hairs, 10-costate, with 5 narrow and low (1 mm. wide and rarely up to 2 mm. high) blunt primary ribs and 5 secondary ribs which are similar but smaller and barely noticeable; pericarp extremely thin and apparently somewhat fragile, yellow when ripe. Seeds probably more than 60, triangular or angulate-ovate in outline, complanate, 12 \times 10 \times 10 mm., 4 mm. thick, in a white pulp.

Brazil. Rio Branco: lower Rio Branco, Tapanaruca, Fróes 23003. British Guiana. Northwestern slopes of Kanuku Mountains, drainage-area of Mokumoku Creek, tributary of Takutu River, alt. 150–400 m., A. C. Smith 3541 (Type). Dutch Guiana. Upper River Corantijne, Hulk 26; River Corantijne, Kaurikreek, Gonggrijp 2111; Stahel & Gonggrijp 3015; River Coppename, Gonggrijp 2565; Placer L'Aiva, Gonggrijp 4126; River Marowijne, Gonggrijp 4101; near Amerikan Kondre, Lanjouw & Lindeman 2304; River Tapanahonie, Jaikreek, Gonggrijp 4117.

Herrania kanukuensis stands rather apart from the other known species of the genus. Its fruit differs strikingly from that of all other species, with the single exception of the unrelated *H. balaënsis* of Ecuador. The capsule is relatively small (measuring 9 cm. \times 5 cm.) with a rounded or very shortly tipped apex (not elongate ovoid or ellipsoid with an acuminate tip, as in most species); the rind is very thin and brittle when dry (in contrast to the usual thick, leathery and fibrous condition), and the ribs are not prominent.

The few fragmentary floral parts which remained adhering to the fruit of *Smith 3541* indicate that there are also floral differences between *Herrania kanukuensis* and other species.

A duplicate type of *Herrania kanukuensis* at Kew has several leaflets which tend to be slightly irregularly dissected, suggesting a condition which approaches that of some specimens of *H. lemniscata* with abnormally developed leaflets. *Herrania kanukuensis* would appear vegetatively to be somewhat intermediate between *H. Mariae* and *H. lemniscata*,

but the indumentum on the under surface is more softly tomentose with brownish stellate hairs than in either H. Mariae or H. lemniscata.

In 1932, Uittien (in Pulle, Fl. Surin. 3: 44. 1932) reduced *Theobroma* Mariae var. lobata to synonymy under *T. Mariae*, identifying all of the then available material from Dutch Guiana as representing this Amazonian concept. In 1943, it appeared to me that the Surinam concept described as *Theobroma Mariae* var. lobata represented the plant which Schomburgk described from nearby British Guiana as Lightia lemniscata, and I placed it in synonymy under *Herrania lemniscata* (Schultes, Caldasia 2: 13. 1943), a species with remarkably lobate leaflets. During the war, the Utrecht material was unavailable for study. Recently, I have had an opportunity of consulting all of the Surinam specimens and am convinced that *Theobroma Mariae* var. lobata and *Herrania kanukuensis* represent the same concept.

From the numerous collections, for the most part from Surinam, it is now obvious that *Herrania kanukuensis* is both a widespread and, at least locally, an abundant element of the flora of Surinam, eastern British Guiana and the adjacent rim of northern Brazil.

The specific epithet *kanukuensis* is derived from the name of the Kanuku Mountains in British Guiana, where the type specimen was collected.

8. Herrania kofanorum R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. 14: 126. t. 28, upper fig. t. 34. 1950.

DISTRIBUTION: Upper Putumayo valley of Ecuador and Colombia.

Small tree, slender and graceful, up to 15 feet tall, usually with one trunk from each root, columnar, apically branched or unbranched, covered with an ashy black scrobiculate and scabrid bark, up to 7 cm. in diameter. Branches ferrugineous-tomentose, becoming almost glabrous, subterete and sulcate. Branchlets similar but more densely tomentose. Leaves at apex of trunk, large, digitate, very long-petiolate, 7-foliolate, stipulate. Stipules caducous, linear, acute, 2.5–3 cm. long, about 3 mm. wide, dry, outside hispidulous or strigillose, inside usually subglabrous. Petioles robust, terete but very obscurely sulcate, basally slightly dilated, subferruginous, very densely and softly tomentose, up to 30 cm. long, 6 mm. in diameter. Leaflets sessile, unequal, lanceolate-oblong, apex with a cusp about 2 cm. long, basally attenuate-decurrent, margin conspicuously and regularly undulate-sinuate; blades firmly coriaceous, mostly 17-30 cm. long, 6-11 cm. wide, above dark green, glabrous or exceedingly sparsely and very minutely strigillose-pilose with caducous white hairs, brownish-hirsute along the principal veins, beneath brownish green, very densely and softly stellate-pilose, ferruginous-tomentose along the principal veins; veins on both surfaces but especially beneath rather prominently raised. Inflorescences fasciculate, up to 20-flowered. Flowers cauline, long-pedicellate, on the lower parts of the trunk, in contracted racemes. Buds large, elongateglobose, 1.8 cm. in diameter, stellate-pilose, rather brownish red. Pedicels

strong, terete, articulate, very densely and minutely stellate-pilose, with ashy-colored hairs, mostly 9-10 mm. long, 1-1.5 mm. in diameter, at the base with small linear, acute and densely tomentose bracts, 2-4 mm. long. Calyx subcymbiform, divided almost to the base. Sepals 3, very strongly unequal, subchartaceous, entire, within minutely papillose, subglabrous and probably eventually glabrous, without sparsely stellate-strigillose, with hairs up to 1 mm. long and also with extremely minute stellate hairs, valvate in bud; the inner 2 sepals elliptic, acute, 10 mm. long, 6 mm. wide; the outer round-ovate, 15-18 mm. long, 15 mm. wide, apically rounded and often deeply (up to 2 mm.) cut, the slit extended interiorly as a furrow nearly to the base. Petals 4 or 5, round-obovate, sessile, concave, strongly cucullate, glabrous, on both surfaces (but especially on the outside) muricate-papillose or granulose, dark red, 5-nerved, striate-nerved with longitudinal purplish veins, ligulate, 9 mm. long, 7 mm. wide. Ligules filiform, pendulous, membranaceous, entirely glabrous but basally minutely granulose, about 1 mm. wide, 80–100 mm. long, at the base strongly dilated. Staminal tube 5-parted, the stamens with alternately 2 and 4 anthers and strongly flattened, short, free filaments. Staminodes conspicuously petaloid, lanceolate-elliptic, acute, basally attenuate, coarsely muricate-papillose on both surfaces, entire, 22 mm. long, 6 mm. wide. Ovary sessile, elongate-ovoid, distinctly 10-ribbed and 5-locular, yellow, very densely stellate-pilose, 2.5-3 mm. in diameter. Pistil flattened, 3 mm. long, glabrous, simple. Fruit unknown, but said to ripen yellow.

Colombia. PUTUMAYO: path between Puerto Ospina and Concepción, alt. 250 m., Schultes 3670. CAQUETÁ: upper Putumayo River, Caucaya, Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 89. Ecuador. Río San Miguel or Sucumbíos, between Río Putumayo and Quebrada Teteyé, alt. 260 m., Schultes 3478 (Type).

Herrania kofanorum differs from its close ally H. balaënsis in being smaller, in having leaflets only half as large, and in having the sepals very conspicuously unequal instead of nearly alike. Herrania kofanorum has two inner sepals which are elliptic, 20 \times 6 mm. and an outer one which is rotund-ovate, $15-16 \times 16$ mm., whereas H. balaënsis has three lanceolate-elliptic sepals which measure 14 \times 6 mm. Furthermore, the outer sepal of Herrania kofanorum is so constructed that it is often conspicuously slit to a depth of 2 mm., and this slit is prolonged as a furrow to the base of the interior of the sepal. (When the split is not present, there is a markedly thin furrow.) Nothing similar is seen in H. balaënsis. Both of these species are closely related to Herrania Dugandii. The specific epithet refers to the Kofán Indians who inhabit the area where the species is known to occur.

9. Herrania laciniifolia Goudot ex Tr. et Planch. Prodr. Fl. Novo-Granat. 209. 1862, nomen subnudum; García-Barriga, Caldasia 1: 55. tt. 1, 4. 1941.

1958] SCHULTES, SYNOPSIS OF HERRANIA 249
 Theobroma laciniifolium (Goudot ex Tr. et Planch.) De Wildeman, Pl. Trop. Grande Cult. 90. 1903.³

DISTRIBUTION: Middle Magdalena Valley, Colombia.

Small tree 12 to 18 feet tall with a simple, erect trunk, about 5 cm. in diameter. Leaves very large, 7-digitate, round in outline, long-petiolate, grouped towards the top of the trunk. Leaflets sessile, strongly patent, the margins deeply pinnatisect with irregular segments (similar to leaves of Carica Papaya), for the most triangular or lanceolate-acuminate, up to 22 cm. long and 3 cm. wide (but usually smaller), papyraceous or membranaceous, basally long-decurrent-attenuate, laciniate towards the apex, the apex itself acuminate, 38–58 cm. long, above sparsely stellate-pilose with suberect hairs along the nerves, the central and lateral veins densely red-tomentulose, beneath rather pale and rather densely and softly stellatepubescent, with the veins as above. Petiole 25-31 cm. long, terete, striate, densely red-tomentulose, basally swollen. Flowers cauline, fasciculate, borne on upper portion of trunk, pedicellate, with the pedicel about 2 cm. long and stellate-pubescent. Sepals 4, lanceolate, rather concave, apically very acute, 17 mm. long, about 7 mm. wide, pubescent on both surfaces, externally with fewer and larger reddish stellate hairs, internally near the apex incanous, with smaller and denser hairs. Petals 5, glabrous, broadly elliptic, very concave, purplish (with yellowish veins) or "greenish white" (Kalbreyer 2047), apically strongly cucullate, ligulate, marginally revolute, 12 mm. long, 8 mm. wide. Ligule filiform, glabrous, red or whitish, 180 mm. long, 1 mm. wide. Staminal tube 5-parted, the stamens all 4-antheriferous. Staminodes petaloid, widely lanceolate, purple, 17 mm. long, 5 mm. wide, the margin slightly sinuous, acute or 3-dentate. Ovary globose or ovoid, 3 mm. long, densely covered with pale yellow hairs. Fruit coriaceous, oblong-ovoid, basally rounded, apically long attenuate-acuminate, the tip itself rather obtuse, 10-costate, the 5 primary ribs conspicuously raised, the 5 secondary ribs much less raised, transversely rugose, brownish red when ripe, 10.5 cm. \times 5 cm. in diameter; peduncle 4 cm. long.

Colombia. [No precise locality], Exped. Bot. Mutisii Novae-Granat. 937; "New Granada, 4,000 ft.", Kalbreyer 2047. CUNDINAMARCA: Peño de Conejo, basin of Río Magdalena, Goudot s. n. TOLIMA: Falán, region of Calamonte, alt. 1120 m., García-Barriga 8375; Mariquita, alt. 547 m., Pérez-Arbeláez 10303.

Herrania laciniifolia is apparently not an abundant element of the flora of Colombia, for it has been collected but thrice in a century, although it grows in one of the most populous parts of the nation. It is most closely allied to *Herrania lemniscata* from which it may be distinguished chiefly by having leaflets which are deeply and regularly pinnatisect (instead of very deeply and irregularly pinnatilobed). The under surface of the

³ This combination has recently been made independently as "*Theobroma lacini-folia*" (Goud. ex Tr. et Planch.) Llano Gómez in "Cultivo del cacao" (Publ. Min. Econ. Nac., Bogota) 19. 1947.

leaflets of *Herrania laciniifolia* is very much more densely and softly stellate-pilose than in *H. lemniscata*; the leaflets are, in general, smaller; and the ligules measure 180 mm. (instead of 85 mm.) in length. The fruit of *Herrania laciniifolia* ripens red, whereas that of *H. lemniscata*, in common with all other species but one, ripens bright yellow. This other exception is *Herrania Camargoana* of the upper Río Negro basin. The fruit of *Herrania Camargoana* ripens scarlet, but this species does not appear to be closely allied to *H. laciniifolia*, and the similarity of fruit color is probably coincidental.

In the collection of Mutis plates preserved at Madrid, there are several illustrations representing *Herrania laciniifolia*. Drawn by Matíz, these are all in black and white, not in color. One plate has a leaf with a complete leaflet and a length of stem with several flowers and buds; another plate has analytical drawings of the flowers and fruits; a third has analyses only of the floral parts.

The Mutis specimen in Madrid (cited above) is sterile, but it was undoubtedly taken from the tree from which the plate was made. In view of the scarcity of collections of *Herrania laciniifolia*, it is unfortunate that a definite locality for the Mutis collection is not available. Both the specimen and the plates agree perfectly with the type and the later material of this remarkably distinct species.

10. Herrania lemniscata (Schomb.) R. E. Schultes, Caldasia 2: 13. 1943; Pittier et al. Cat. Fl. Venez. 2: 134, 139. 1947; R. E. Schultes,

Bot. Mus. Leafl. Harvard Univ. 13: 281. t. 30. 1949.

Lightia lemniscata Schomb. Rep. Assoc. Advancem. Sci. 13: 71. 1844. Nomen subnudum.

DISTRIBUTION: British and Dutch Guiana and the Orinoco basin of eastern Venezuela, extending into northeastern Colombia.

Small tree, with a simple, round, slender trunk up to 30 feet tall, with leaves grouped at the tip of the trunk. Branches apparently tomentose, becoming subglabrous. Leaves very large, 7-digitate, very long-petiolate, stipulate. Stipules caducous, minutely subulate, extremely densely and softly ferruginous-tomentose, about 2 cm. long, basally 2 mm. wide. Petioles robust, terete, sulcate, apically widely complanate-flabelliform, very densely and softly rusty tomentose, slightly swollen then immediately strongly constricted, up to 45 cm. long, 8-10 mm. in diameter. Leaflets sessile, unequal, the central one up to 80 cm. long, 40 cm. wide, acuminate, basally long-decurrent-attenuate, the margin very profoundly pinnatilobate with (usually) 4 irregular, usually triangular or broadly lanceolateacuminate segments, in the longest part of leaflet up to 18 cm. long, 9-10 cm. wide, papyraceous or membranaceous, above dark green, subglabrous or beset with very remote stellate hairs, densely ferruginous-strigillose along the nerves, beneath pale green, densely and softly stellate-pilose, the nerves densely ferruginous-tomentose, the veins prominent on both surfaces. Inflorescence fasciculate, bearing probably up to 30 or 40 (but

usually about 20) flowers. Flowers borne in contracted racemes on the lower portion of the trunk, dark crimson-purple, pedicellate. Pedicels strong, terete, minutely and densely stellate-tomentellose, articulate, 7-8 mm. long, basally subtended by a short, linear, tomentose bract, 1 mm. long. Buds globose, 9-10 mm. in diameter, very densely and minutely stellate-tomentellose and stellate-pilose. Calyx divided almost to the base, subcymbiform. Sepals 3, reflexed, almost equal, thick, internally very densely puberulent, externally very densely stellate-tomentose and stellatepilose (2 distinct types of hairs), with an entire and strongly inflexed margin, brownish red; the two larger sepals ovate, subobtuse, 12-13 mm. long, 7 mm. wide; the smaller one lanceolate-elliptic, apically subobtuse, 13-15 mm. long, 5-8 mm. wide. Petals 5, sessile, elongate-obovate, concave, strongly cucullate, entire, dark blood-red (sometimes possibly yellowish) with 5 prominent black or purplish nerves, 6-7 mm. long, 4 mm. wide, glabrous, on both surfaces but densely muricate-papillose externally, thick, ligulate. Ligules hanging, membranaceous, filiform, glabrous, without nerves, basally 1-1.5 mm. wide, about 85 mm. long, blood-red, sometimes becoming yellowish. Staminal tube 5-parted with stamens alternately 2and 4-antheriferous, filaments short, free and simple. Staminodes conspicuous, petaloid, dark blood-red, sometimes apically yellowish, elliptic, slightly and obscurely undulate, acuminate, 10-12 mm. long, 4-5 mm. wide, glabrous, densely muricate-granulose on both surfaces. Ovary sessile, ovoid-globose, 4.5-5 mm. long, 2.5 mm. in diameter, distantly 10-costate with 5 primary and 5 secondary ribs, yellow, very densely hispid-pilose. Style terete, glabrous, simple, with an obscurely 5-parted stigma. Fruit long pedunculate (with a strong, glabrous or glabrescent peduncle up to 4.5 cm. long and 3 mm. in diameter) perfectly ovoid, 7 cm. long, 4 cm. in diameter, apically very shortly and abruptly cuspidate, basally almost rounded, densely and minutely stellate-puberulent, apparently lacking stinging hairs, 10-costate with 5 narrow, comparatively low, subcultriform primary ribs which are 2 to 4 mm. high and 1-2 mm. thick (in the dried specimen) and 5 similar but smaller ribs, the very thin pericarp strongly reticulate-costate between the longitudinal ribs, probably yellow when ripe. Seeds apparently more than 60, triangular or angular-ovate in outline, flattened, 12 \times 11 \times 11 mm., above 4 mm. thick, buried in a white pulp.

British Guiana. Banks of Barima River. Schomburgk s. n. (Type); [no precise locality], im Thurn s. n. (Type of fruit); Essequibo River, White Creek, Groete Ck., Forest Dept. Brit. Guian. Field No. F1763, Research No. 4500. Colombia. SANTANDER: 15 km. east of Puerto Berrio, alt. about 250 m., Scolnick, Araque & Barkley 195001. Venezuela. Near mouth of Orinoco River, Rusby & Squires 252; Pakaraima Mountains, Myers 3371. Bolívar: Salto de Pará, Medio Caura, alt. 120 m., L. Williams 11339; lower part of Quebrada O-paru-mo, tributary of Río Pacairao, below Santa Teresita de Kavanayen, alt. 915–1065 m., Steyermark 60558.

Herrania lemniscata is undoubtedly one of the most strikingly distinct species of the genus. It can be distinguished at once by its very large and

JOURNAL OF THE ARNOLD ARBORETUM 252 VOL. XXXIX broad leaves with pinnatilobed leaflets. It is, apparently, most closely related to H. laciniifolia of central Colombia, but its leaflets are much more coarsely incised, with fewer and wider lobes. Florally, H. lemniscata does not seem to be very distantly allied to H. Mariae and H. kanukuensis.

It would appear that the Guianan Herrania lemniscata occupies a somewhat intermediate position between the Colombian H. lacinifolia on the one hand and the Amazonian H. Camargoana on the other. This relationship has been discussed under the latter species.

The name Lightia lemniscata was published by Schomburgk in 1844 without an adequate description and without the citation of specimens. It must be considered a nomen subnudum. Several years later, Schomburgk (Linnaea 20: 756. 1847) reduced the name to synonymy under Herrania Mariae, and, wishing to perpetuate a generic name honoring Governor Light of British Guiana, he transferred the name Lightia to a new genus in another family. In 1848, he (Schomburgk, Fauna und Flora von British-Guiana. 993. 1848) listed under Herrania Mariae specimen(s) which he had collected in British Guiana along the River Barima and its affluents. It is probable, then, that this represents the area from which the type material of Lightia lemniscata came.

Fortunately, I have had an opportunity to study a beautiful collection (Archer 2514) from this same region. I have considered it as a topotype, although it must be remembered that Schomburgk's mention of the "River Barima and its affluents" circumscribed a rather extensive area.

All of the material of Herrania from British Guiana and northeastern Venezuela which I have seen is (with exception of collections from near the Brazilian border) referable to one species. This species is distinct from others of Middle and South America. I am inclined to believe that these specimens are referable to the concept which Schomburgk called Lightia lemniscata.

In the New York Botanical Garden there is a specimen collected in the easternmost part of Venezuela near the mouth of the Río Orinoco in 1896 (Rusby & Squires 252). On the label of this specimen, a handwritten notation states: " = coll. by Schomburgk in Brit. Gui." On the basis of this annotation and the near homogeneity of the Guianan collections, I validated Schomburgk's nomen subnudum and transferred it to the genus Herrania in 1943.

When I validated the Schomburgk concept, making the new combination Herrania lemniscata, European collections were unavailable for study. Recently, additional and extensive material which I have seen in England indicates that Herrania lemniscata is indeed a very distinct species. Schomburgk's original water-colors, made in the field, are preserved at the British Museum (Natural History). Included in the collection is an excellent painting of this concept (as Lightia lemniscata) which depicts with unusual accuracy the habit of the small tree. There is, likewise, what appears to be a Schomburgk water-color attached to one of the herbarium sheets at Kew.

The collection Myers 3371 consists only of flowers. It is referred with some reservation to Herrania lemniscata. The collection L. Williams 11339 has been reported in the literature (L. Williams, Exploraciones botánicas en la Guayana venezolana. 309. 1942) as Herrania Mariae. By using the specific epithet lemniscata, Schomburgk intended to call attention to the very long ribbon-like ligules which adorn the flower.

Herrania Mariae (Mart.) Decaisne ex Goudot, Ann. Sci. Nat. III.
 2: 233. 1844.

Abroma Mariae Mart. Denkschr. Regensb. Bot. Gesell. 3: 297. tt. 6, 9. 1841.
Theobroma Mariae (Mart.) Schum. ex Mart. Fl. Brasil. 12(3): 71. t. 15.
1886; Ducke, Rodriguesia 4: 273. t. 5, fig. 2. tt. 6, 7. 1940.

DISTRIBUTION: General in the Amazon basin, with the exception of the northern and northwestern sectors.

Small or large tree, up to 30 (doubtfully up to 60) feet tall; trunks (often 5 or 6 from a root) erect, columnar, 7-30 cm. in diameter, with brownish-black or black, rimose or scrobiculate bark. Branches sometimes closely crowded, forming a subglobose crown, in which the lower branches are subhorizontally spreading, rather flexuous, sometimes few and wide-patent; ferruginous-tomentose but becoming subglabrous, subterete, sulcate. Branchlets similar, spreading. Leaves large, digitate, long-petiolate, 6-9 (usually 7-) -foliolate, stipulate. Stipules caducous, linear, acute, 2.5-4 cm. long, about 3 mm. wide, dry, tomentose. Petioles strong, terete, subsulcate, basally somewhat swollen, 30-50 cm. long, 7 mm. in diameter, subferruginous, very densely and softly tomentose with erect, brown, stellate hairs. Leaflets thin-membranaceous to thin-papyraceous, sessile, unequal, usually strongly rhomboid-ovate, apically acuminate (acumen about 2 cm. long), basally attenuate-decurrent, entire or very slightly subundulate towards the apex and conspicuously armed with small, spinelike, hirsute, mucronulate prolongations of the veins up to 1 mm. long; the leaf surfaces usually 27-54 cm. long; 7-19 cm. wide, above dark green, very sparsely and minutely hirsute (or, in rare specimens, subglabrous) with white hairs (very rarely with brownish stellate hairs), more densely hirsute along the principal veins and along the margin, beneath pale green, subasperous or soft with minute stellate-sericeous hairs, ferruginous-tomentose along the principal veins; the veins prominent on both surfaces, but conspicuously elevated beneath. Inflorescences fasciculate, usually fewflowered (with about 10-15 flowers) but frequently many-flowered (80-90). Flower buds subglobose, large, 17 mm. in diameter, densely stellatehispid. Flowers cauline, long-pedicelled, growing from the middle and lower portions of the trunk in contracted racemes. Pedicels densely fulvotomentose, hispidulous with minute, appressed strigillose hairs and also sparsely setose, articulate, 1.5-5 cm (mostly 3.5-5) long, basally subtended with a short linear, acute, densely tomentose bract 3 mm. long. Calyx subcymbiform, divided nearly to the base. Sepals 3-5, strongly unequal, entire, externally densely stellate-strigose, internally glabrous,

254 JOURNAL OF THE ARNOLD ARBORETUM [VOL. XXXIX

or very minutely pilose, thick-membranaceous, brown, valvate in bud later reflexed, longitudinally striate; the interior broadly elliptic-oblong, apically subacute, with coarse hairs frequently up to 1 mm. long, 12-15 mm. long, 6–10 mm. wide; the exterior very broadly rotund or broadly ovate, apically abruptly and obscurely acuminate, with coarse hairs 1 mm. long, 11-13 mm. long, 11-12 mm. wide. Petals 4 or 5, basally sessile, concave, rotund-obovate, apically very strongly cucullate, 7-9 mm. long, 6-8 mm. wide, glabrous, muricate-papillose on both sides, 5-nerved, pale purplish red with black or purple veins, apically ligulate. Ligules filiform, pendulous, membranaceous, pale yellow or white, with purple venation, minutely granulose in all parts but especially so at the base, basally up to 4 mm. and apically hardly 1 mm. wide, 75-100 mm. long (very rarely less), apically slightly coiled. Staminal tube 5-parted, stamens alternately 2and 4-antheriferous, filaments short and free, anthers yellow. Staminodia conspicuous, petaloid, reflexed, red, lanceolate or lanceolate-elliptic, apically obtuse and usually indentate mucronate or serrate, somewhat sinuateundulate, glabrous, muricate-granulose on both sides, up to 20 mm. long, 6-7 mm. wide. Ovary sessile, elongate-subglobose, pentagonal (distinctly 10-costate and 5-locular), densely stellate-pilose, rose-colored or yellowwhite. Style short, subcylindric-pentagonal, reddish. Stigmas 5, filiform, rose-colored. Fruit baccate, elliptic-ovoid, apically acuminate, longpeduncled (peduncle up to 2.5 cm. long), conspicuously 10-costate; the 5 primary ribs large, protruding, acute-scutelliform, about 8 mm. tall, 5 secondary ribs similar but smaller, about 4 mm. tall, conspicuously fibrousstriate transversely between the ribs, very densely stellate-hispid with stinging hairs along the ribs, up to 10-12 cm. long, 6-7 cm. in diameter, pericarp thick, subsucculent (not conspicuously fibrous), yellow when ripe. Seeds 30-40 (possibly -60), obtusely rhomboid, flattened, with a subcoriaceous testa, about 10 cm. long, 9 mm. wide and 4 mm. thick, in a white, acidulous pulp.

Brazil. AMAZONAS: Rio Solimões, von Martius s. n. (Type); Paleta, Teffé, Krukoff's 4th Exped. Brazilian Amazon 4523; Fonte Bôa, Fróes 20630; Rio Jurua, Marary, Ule 5031; Rio Amazonas, Taperinha, near Santarém, Ginzberger 804; Rio Madeira, Humayta, near Tres Casas, Krukoff's 5th Exped. Brazilian Amazon 6085; Riosinho, Juruema, Fróes 21041. PARA: Belém, Ducke 595; Museu Goeldi, Murça Pires & Black 740; Utinga, Schultes 8072; Belterra, Black 47-1916. Colombia. AMAZONAS: Trapécio Amazónico, interior regions of trapecio between Amazon and Putumayo watersheds, alt. about 100 m... Schultes 6759; mouth of Río Atacuari, Black & Schultes 46-223. Peru. MADRE

DE DIOS: near Iberia, Schultes 6461.

Due primarily to the detailed drawing of *Herrania Mariae* which was published in *Flora Brasiliensis* and to the general availability and reliability of this work, botanists have had a tendency to consider as representing this species collections from a wide area but which actually belong to very diverse concepts. Almost all collections in our herbaria have been referred to *Herrania Mariae*. Indeed, very recently, Ducke has stated that *Theo*-

broma Mariae is "the only species in the Brazilian Amazonia representing the subgenus (or section) Herrania . . . ," that this "species is found throughout the hylea (including the Guianas) . . . ," and that "it is probable that, in addition to atrorubra, still other species of the subgenus Herrania, described from northern and northwestern South America, will in the future be reduced to synonymy under Theobroma Mariae" (Rodriguesia 4: 273. 1940).

Herrania Mariae is probably the tallest species in the genus and, unlike almost all other species (except H. pulcherrima), it often has many trunks growing from one root. Martius described the plant as being 20-30 feet in height, and the drawing which was published with the original description shows an extremely robust and corpulent tree with a basal diameter of some 15-30 cm. and with a very heavy, round and full crown. My field work with Herrania leads me to believe that this drawing, herein reproduced for historical reasons, is erroneous and greatly exaggerates the size of the trunk and crown. Ducke commented similarly on this illustration when he wrote (loc. cit.), "In Martius' drawing, reproduced in 'Flora Brasiliensis,' Th. Mariae appears as a much-branched tree which does not in any way correspond with the real habit of our plant" The few collections of this widespread species which are at hand at the present time exhibit some variation, but an abundance of comparative material is lacking for determining with precision the character and extent of the variation. I am certain that when more abundant collections and field observations have been made, it will be necessary to recognize several definite geographical variants. An example of our inability to treat with complete certainty some collections is seen in Krukoff 6085 which may possibly be an hybrid between Herrania Mariae and H. nitida. Schultes 6238 and 6461, unfortunately sterile, represent perhaps one of the extremes exhibited by the available material of Herrania Mariae. They are the southernmost collections of the genus, occurring on high land which never floods (in contrast to the flood-land habitat of the banks of the Amazon), and appear to have on the under surface of the leaflets a much denser and softer indumentum which tends to be rather greyish in life. In the herbarium at Munich, there are seven very ample specimens of Martius' type collection. A study of this material has enabled me to evaluate the concept more critically. The type material has extremely membranaceous to very thinly papyraceous leaflets which have a rather softly asperous indumentum on the lower surface and a sparse asperous pilosity on the upper. The leaflets are strongly rhomboid-obovate, a shape which is peculiar to Herrania Mariae. The petiole, shorter and less robust than in most species, is densely tomentose, and the inflorescence is manyflowered. Herrania Mariae is related to H. Cuatrecasana, H. nitida and H. pulcherrima. All four species have a similar type of fruit with very large and protruding cultriform ribs which are unequal and with strong transverse wrinkles between the ribs and more or less at right angles to them. Herrania Mariae resembles H. Cuatrecasana very closely in some char-

256 JOURNAL OF THE ARNOLD ARBORETUM [VOL. XXXIX

acters, and I once suspected that the latter might well be considered a variety of the former. Further field work and additional collections of Herrania Cuatrecasana, however, and the discovery of H. Mariae var. putumayonis give us reason to maintain the two concepts as completely distinct. The most obvious difference between the two species is the shape of the leaflets: very long oblanceolate-oblong and very long and gradually attenuate towards the base in Herrania Cuatrecasana and rhomboidobovate and more abruptly attenuate towards the base in H. Mariae; the leaflets of the former are also usually very much longer than those of the latter species, and the petiole is much longer, stouter and more softly ferruginous-tomentose. Herrania Mariae has lanceolate or lanceolateelliptic, somewhat sinuate-undulate and apically often serrate or indentatemucronulate staminodes which are, for the most part, 20 mm. long and 6-7 mm. wide, whereas H. Cuatrecasana has definitely rhomboid-lanceolate, entire and apically non-serrate staminodes which measure 25 mm. long and 8 mm. wide. The ligule of the former species usually measures from 75 to 100 mm. in length, of the latter, 130 mm. The differences which set Herrania Mariae apart from H. nitida are very evident. The latter is separated at once from the former by its complete lack of indumentum on the leaflets (or, when slightly tomentulose underneath, by the sparsity and asperous nature of the hairs); by its leaflets which are usually lanceolate-elliptic, more firmly chartaceous and most often entire; and by a number of floral characters.

Herrania pulcherrima is most easily separated from H. Mariae by the enormous size of its leaflets (up to 60 cm. long) which are oblong, for the most part about half as wide or wider, with the secondary and tertiary veins extraordinarily conspicuous and raised beneath, giving the upper surface, in most specimens, a verrucose appearance; by the unusually long and strong petioles; and by the larger flowers which are dark red in all parts, excepting the ligules which in some specimens are cross-banded scarlet and whitish. Both of these species have a characteristically trifid staminode.

With the specific epithet of *Herrania Mariae* Martius honored Maria, Queen of Saxony, whose father, King Maximilian Joseph of Bavaria, patronized Martius' extensive botanical explorations in South America.

Van Hall (Cacao. ed. 2. 74. 1932) states that seeds of this species are occasionally found as an adulterant in "Pará cacao", but it is not certain that his identification can be taken as reliable: his confusion of *Herrania Mariae* with another species is obvious from the statement that "it is very common in the forests of Surinam near Paramaribo and also deep into the interior" (loc. cit.).

11a. Herrania Mariae (Mart.) Decaisne ex Goudot var. putumayonis
 R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. 14: 129. t. 30, upper fig. 1950.

DISTRIBUTION: Western part of the Amazon Valley, especially in the Putumayo River basin.

Small tree up to 12 or 14 feet tall, differing from *Herrania Mariae* chiefly in having much larger (up to 52 cm. long, 18 cm. wide), lanceolate-elliptic (not conspicuously rhomboid) leaflets; stronger and longer petioles; larger flowers up to 17 mm. in diameter, with the buds globose, and shorter ligules up to 70 mm. long, but usually somewhat less.

Brazil. Амаzonas: Rio Jurua, Lago Cerrado, Traill 65. Peru. LORETO: Río Putumayo, between Río Igaraparana and Río Yaguas, alt. 100–150 m., Schultes 4010 (Туре).

Additional material may indicate that this concept is deserving of specific rank. At the present time, however, it would seem advisable to treat it as representing a variety of *Herrania Mariae*. The fruit of *Schultes 4010* is hardly distinguishable from that of typical *Herrania Mariae*. The flowers have several differentiating characters, the most conspicuous of which is the shorter ligule. Vegetatively, the collection is extremely similar to *Herrania nycterodendron* (with the type plant of which it was growing) and differs markedly from *H. Mariae* chiefly in the departure from the typical rhomboid form of the leaflets and in their unusually large size. The type plant of *Herrania Mariae* var. *putumayonis* consisted of four or five trunks in a clump, whereas *H. Mariae* is a treelet with a single trunk, although the condition of several trunks from one root is not uncommon in *H. Mariae*.

In the Paris herbarium there is a specimen, the collector and date of which we are ignorant, referable with reservation to *Herrania Mariae* var.

putumayonis. It was collected at the upper Amazon town which is now called Teffé: "fluv. Amaz. Ega. 2660. Abroma n. sp. Arbor debilis." The specimen is sterile, but it was thus early recognized as a distinct concept. Herrania Mariae var. putumayonis may represent a western variant of the species which is most abundant in the eastern half of the Amazon basin. The varietal epithet refers to the Putumayo River.

12. Herrania nitida (Poepp.) R. E. Schultes, Caldasia 2: 16. t. pag. 17. 1943.

Abroma nitida Poepp. in Poepp. & Endl. Nov. Gen. ac Sp. Pl. 3: 73. 1845. Brotobroma aspera Karst. & Tr. ex Tr. Nuev. jén. y esp. pl. fl. Neo-Granat. 12. 1854.

Herrania aspera (Karst. & Tr. ex Tr.) Karst. Linnaea 28: 447. 1857.
Theobroma nitidum (Poepp.) Schum. ex Mart. Fl. Brasil. 12(3): 72. 1886.
Non T. nitida Bernoulli, Neue Denkschr. all. Schweiz. Gesell. gesam.
Naturw. 24(3): 15. t. 17, fig. 3. 1871.
Herrania atrorubens Hub. Bull. Soc. Genève II. 6: 187. 1914.
Theobroma aspera (Karst. & Tr. ex Tr.) Van Hall,⁴ Cacao. ed. 2. 49. 1932.

⁴ This combination was made, but imperfectly so, by van Hall who, in a key, refers to "T. aspera (Karsten) Schumann". He refers to Schumann's account in Martius' Flora Brasiliensis where aspera is not mentioned under *Theobroma*, Herrania or Brotobroma; and there is no evidence that Schumann ever made the combination.

JOURNAL OF THE ARNOLD ARBORETUM [vol. XXXIX
 Herrania nitida (Poepp.) R. E. Schultes var. aspera (Karst. & Tr. ex Tr.)
 R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. 14: 130. 1950, pro parte.
 DISTRIBUTION: Widespread in the western half of the Amazon Valley
 and the Orinoco basin in Colombia.

Small tree, rather weak, graceful, probably up to 12 feet tall, with dark brown, roughened bark; the trunk usually less than 7 cm. in diameter at the base. Branches sparsely and minutely tomentose, becoming glabrous. Petioles subcomplanate, conspicuously striate-sulcate, ferruginous, very minutely closely appressed stellate-tomentulose, basally somewhat swollen, up to 40 cm. long, 5 mm. in diameter. Leaves grouped at the apex of the trunk, 7-9-digitate, long-petiolate, stipulate. Petiole usually slender, asperous, very minutely ferruginous-tomentulose, sometimes becoming subglabrous, terete but very deeply sulcate, up to about 40 cm. long, basally 4-5 mm. in diameter. Stipules linear, up to 2.5 cm. long, 1 mm. wide, usually brown stellate-setulose. Leaflets sessile or nearly so, unequal, lanceolate-oblong, acuminate, basally very long attenuate-decurrent, marginally entire, rigid-chartaceous to subcoriaceous, light green, shiny, glabrous above, glabrous or rarely with very sparse and deciduous minute stellate hairs remotely placed along the nerves beneath; the central leaflets 25-45 cm. long, 7–14 cm. wide; the lateral leaflets much smaller and often asymmetrical. Inflorescence fasciculate; often very numerous on the basal portion of the trunk, up to 30–40-flowered. Flowers cauline, pedicellate. Pedicels articulate, densely appressed, tomentulose with occasional strigose setae, 5 mm. long, less than 1 mm. wide. Calyx subcymbiform. Sepals 3, yellow-red, externally very coarsely stellate-setose, internally glabrous; outer sepal rounded-ovate, or triangular-ovate, up to 14 mm. long 10 mm. wide (but usually smaller); inner sepals elliptic, acute, up to 17 mm. long (but usually shorter) 6 mm. wide. Petals 5, broadly obovate, rotund, 4-5 mm. long, 4-5 mm. wide at the top, strongly cucullate, fleshy membranaceous, very densely muricate-papillose on both sides but especially without, glabrous, longitudinally marked with 5 or 6 dark red veins, yellowish-rose or rose-white, ligulate. Ligules linear, hanging, basally slightly contracted, apically slightly coiled, pink or scarlet, up to 80 mm. long, membranaceous, glabrous, longitudinally marked with five purple nerves. Staminal tube 5-parted, alternately 2- and 4-antheriferous with simple, flattened, free filaments. Staminodes conspicuous, petaloid, glabrous, muricate-granulose, elliptic, acute, marginally slightly undulating, dark blood-red without, yellowish-red within, 9 mm. long, 5 mm. wide. Ovary 5-locular, subcylindric, densely and very minutely stellate-pilose, yellow, about 1.8 mm. long, 1 mm. in diameter. Style strongly flattened, 3 mm. long, with a simple stigma. Fruit baccate, ovoid, acuminate, 11 cm. long, 5 cm. in diameter, dull, rich green, 10-costate, the 5 primary ribs thin, cultriform, basally up to 2.5-3 mm. and apically 1.5 mm. thick, 8-9 mm. high, the 5 secondaries similar but smaller, minutely and very densely beset with stinging hairs along the ribs; pericarp between the ribs usually smooth and not fibrous-rugose, very thin, sometimes with a few stinging hairs but becoming glabrescent. Peduncle short and strong, usually under

14 mm. long, 2.5 mm. in diameter. Seeds 30–40 or more, flattened, roughly triangular in outline, 9 mm. \times 8 mm. \times 5 mm., in a white pulp.

Brazil. Амаzonas(?): Glaziou 9635. Амаzonas: Rio Purus, varzea at Sobral, Traill 64; Rio Solimões, Santo Antonio do Iça, Ducke 7618; Benjamin Constant, Fróes 20919; Amaturá, Ducke s. n.

Colombia. AMAZONAS: Río Amazonas, La Victoria, L. Williams 2816, 2843; Leticia, alt. about 100 m., Schultes 6000, 6016, 6141, 6142, 6143, 6144, 6145, 6146, 6147, 6149, 6192a; Río Loretoyacu, Schultes 6304, 6045, 6058, 6118, 6124, 6640, 6878, 8129, Schultes & Black 8286, 8377; Río Apaporis, between Río

Pacoa and Río Kananarí, region around Soratama, alt. 250 m., Schultes & Cabrera 13628, 13630, 13632, 14880, 14882; Schultes & García-Barriga 14016; Río Caquetá, La Pedrera, Schultes 5876; Anglo-Colombian Cacao Collecting Expedition (Baker & Cope) 17, 19, 22, 24. CAQUETA: Río Orteguaza, Tres Esquinas, Schultes 3698; upper Río Putumayo, Montclar, Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 85; Caucaya, Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 87, 88; Río Caucaya, Laguna Primavera, Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 92; Río Caguan, Arbolitos, Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 100; Camp Three, Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 112; Cartagena, Anglo-Colomb. Cacao Coll. Expedition (Cope & Holliday) 106; Río Caqueta, Camp Five, Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 120. PUTUMAYO: Río Putumayo, Puerto Ospina, alt. about 280 m., Schultes 3405, Schultes & Cabrera 18933; Río Caucaya, Schultes 3730. VAUPÉS: upper Apaporis basin, path between Río Itilla and Río Macaya, alt. 300 m., Schultes 5351; Río Macaya, Cachivera del Diablo, alt. 350 m., Schultes 5491; near confluence of Río Ajaju and Río Macaya, Puerto Hevea, alt. 350 m., Schultes 5529; middle Apaporis basin, Río Kananarí, Buenos Aires, alt. about 250 m., Schultes 5685; Río Apaporis, Jinogoje, Anglo-Colomb. Cacao Coll. Exped. (Baker & Cope) 10; Río Vaupés, Puerto Naré, Schultes 5359; near Miraflores, Schultes 5715; La Jirisa, Schultes 5755; near mouth of Río Kubiyú, Schultes & Cabrera 14537; Circasia, alt. 800 ft., Schultes & Cabrera 19665; between Mitú and Javareté, Igarapé, Murutinga, near Tipiaca, Schultes & Cabrera 19284; Río Kuduyarí, Cerro Yapobodá, Schultes & Cabrera 14343; near Irabasú, Schultes, Baker & Cabrera 18439; lower course of Río Kuduyarí, alt. 700-800 ft., near Yararacá. Schultes, Baker & Cabrera 18553; Río Paca, Wacaricuara, Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 55c; Río Inirida, Caño Caribe, Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 67; Río Papunawa, near junction with Río Inirida, Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 76. МЕТА: Villavicencio, alt. 400 m., Triana s. n., Killip 34247; Llanos de San Martín, near Villavicencio, alt. 400 m., Triana 5333; Cordillera La Macarena. path between Río Guejar and Caño Guapayita, Cano Yerly, Idrobo & Schultes 768, Schultes 11627; savannahs near San Juan de Arama, Río Guejar, near

landing strip "Los Micos", alt. about 500 m., Idrobo & Schultes 1325. Ecuador. Río Pastaza, near Andrés, Spruce 4969.

Peru. [No precise locality], "Herb. Pavon". SAN MARTIN: Río Tocache, Poeppig 1979 (Type). LORETO: Río Marañón, near Pongo de Manseriche, Tessmann 4024; Iquitos, alt. about 100 m., Killip & Smith 27431, Murça Pires & Black 873; lower course of Río Huallaga, between Yurimaguas and Balsopuerto, alt. 135–150 m., Killip & Smith 28234; Río Amazonas, Caballo Cocha, L. Williams 2332; upper course of Río Itaya, San Antonio, alt. 145 m., L. Williams 3345; Paraíso, alt. 145 m., L. Williams 3364.

260 JOURNAL OF THE ARNOLD ARBORETUM [VOL. XXXIX

Herrania nitida is the most widespread species in the genus, extending from the eastern slopes of the Andes in Colombia, Ecuador and Peru throughout the entire Amazon basin, being especially concentrated in the western half. As should be expected, therefore, there is evident considerable variation within the concept. It is undoubtedly the most variable species of Herrania, and further collections and studies will probably indicate that some of the variations are deserving of taxonomic recognition. To date, however, I have been able to separate out only one variant which is recognized now as a forma. One can think of Herrania nitida as a kind of evolutionary center. It is in itself most distinct from all other species, but in certain respects some of its variants approach the variants of other species. Its foliage resembles that of Herrania albiflora and H. purpurea to a remarkable degree, but there are no floral or fruiting characters which point to even a remote relationship. Herrania nitida has often been confused with H. Mariae, usually because, in spite of its specific epithet, it has variants with leaflets softly tomentose (even though always sparsely so), especially in the central and eastern parts of the Amazon Valley. Indeed, one collection (Krukoff 6085) is so intermediate between these species that I have indicated (under Herrania Mariae) that it may possibly represent a hybrid of the two. Very significant floral characters (coloration, size and shape of the staminodes, form of the style, and placement of the anthers) serve easily to set the two apart; and the peculiar rhomboid-obovate leaflets of Herrania Mariae contrast strikingly with the lanceolate-oblong leaflets of H. nitida. We

can see from the similarity in the fruit, however, that these two species are more closely allied than one would suspect from a study of the floral and vegetative parts.

The flower of *Herrania nitida* is one of the smallest and most delicate in the genus. Usually there is a general tendency in the staminodes and even in the petals for a yellowish tinge, with nerves which are the more conspicuous in these parts because of their dark purplish color against the yellow. The ligules are almost always yellowish or white in the upper half, but there are variants which have very dark scarlet ligules. The leaflets of *H. nitida* are generally drooping, a characteristic which I have not seen commonly in other species.

Herrania nitida prefers well-drained sloping soil, usually of a semilateritic consistency, and is rarely found where the annual flood of the rivers remains long enough and becomes deep enough to produce a drowning effect. It is most often rather abundant in the areas where it occurs.

In 1950, when I reduced *Herrania aspera* to a varietal status under H. *nitida*, I pointed out that there has been confusion in the presentation of this concept since 1857, when Karsten stated that it was found "in vallis Orenocensis marginibus ad pedem Andium bogotensium meridensiumque . . . et littora fluminis Magdalenae". It was difficult to accept the occurrence of the same species on both sides of the great Andean cordillera, and Karsten's assertion may have been based on the study of a sterile specimen of *Herrania albiflora* Goudot. Later, Triana and Planchon (Prodr. Novo-

Granat. 209. 1862) erroneously reduced Herrania aspera to synonymy under *H. pulcherrima* Goudot. A further confusion resulted with my treatment of Herrania aspera as a variety of *H. nitida*.

A study of the fruit and flowers of the Macarena material indicates that this plant, which represents a hitherto undescribed concept and which has, in part, been referred in the past to H. aspera, bears little relationship to Herrania pulcherrima and none to H. nitida. The confusion which has resulted in the past appears to be directly a result of two factors: incomplete material and Karsten's failure to cite a definite specimen which we could take as a type. The presumed type of Herrania aspera has been taken as Triana 5333 from the llanos of Villavicencio. In view of the material now available and of field studies in the Macarena not far from the type locality of Herrania aspera, I am now reducing H. aspera to synonymy under H. nitida and am describing H. tomentella to accommodate the soft-pilose, large-leaved plant which is common in the western part of the Llanos and in the Macarena. Herrania atrorubens is also herewith reduced to synonymy under H. nitida. When Huber described Herrania atrorubens, he cited his collection 7935 from the Alto Amazonas of Brazil as the type and only material of the concept. He stated that it differed from Herrania Mariae in being smaller and in having dark red flowers. In 1944, in treating this binomial (Caldasia 2: 329. 1944), I wrote, "I have been unable to examine the type of this concept. Without typical material, I have found it impossible to estimate its validity as a species, but it would seem that the colour character alone would hardly suffice for the creation of a new specific concept." Now, having completed an extensive study of the classical material of the genus, I have been unable to locate the type of Herrania atrorubens. One would expect it to be preserved in the Museu Goeldi in Belém do Pará or in the Herbier Boissier in Geneva, but a search in these two institutions, as well as in other principal Brazilian and European herbaria has not uncovered Huber's material. In the light of the experience gained during the study of a wide range of material, it would seem from an evaluation of the meager characters given by Huber and from the geographical data given for the type collection that Herrania atrorubens may be reduced safely to synonymy under H. nitida.

12a. Herrania nitida (Poepp.) R. E. Schultes f. sphenophylla R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. 14: 131. 1950.

Herrania nitida (Poepp.) R. E. Schultes var. sphenophylla R. E. Schultes, Caldasia 2: 20. 1943.
?Theobroma Mariae (Mart.) K. Schum. f. minor Diels, Notizbl. 15: 48. 1940.
DISTRIBUTION: Western part of the Amazon Valley.

A small tree which differs from *Herrania nitida* principally in having smaller and lanceolate-elliptic or very narrowly obovate leaflets, in having a fewer-flowered inflorescence, in having flowers which are usually larger JOURNAL OF THE ARNOLD ARBORETUM [vol. xxxix and redder (the ligules usually entirely red), in having a smaller fruit (7.5–8 cm. long, 4 cm. in diameter), and in being humbler in stature.

Brazil. Амаzonas: Rio Jutahy, Riosinho Jurunema, Fróes 21040. Colombia. PUTUMAVO: Umbría, alt. 325 m., Klug 1853. Амаzonas: Trapécio Amazónico, Río Loretoyacu, Black & Schultes 46-331. Peru. Loreto: Río Ucayali. Tessmann 3287; Guamitanacocha, Río Mazán, alt. 100-125 m., Schunke 45 (Type).

The very striking difference in size between the leaves and nearly all other parts of Herrania nitida and H. nitida f. sphenophylla cannot be laid to ecological variation. When this difference was first noted (on the basis of Schunke 45) it was recognized as varietal. Later studies in the field, however, as well as information obtained through an examination of additional collections, indicate that the concept is probably better treated as a form, since little other than color and size differences, constant though they be, are evident. In 1940, Diels described Theobroma Mariae f. minor from the Río Pastaza in eastern Ecuador. The type specimen seems to have been destroyed during the recent war. If we may judge from the few characters given in Diels' original description and from geographical distribution, it might be safe to assume that the concept represented either Herrania nitida or, more probably, H. nitida f. sphenophylla. In 1943, I pointed out this possibility (Caldasia 2: 332. 1944), stating: "I have been unable to examine herbarium material or photographs of this form, and, until an opportunity to do so presents itself, I shall be unable to treat it critically. In most of the characters enumerated in the original description, it would seem that . . . it approaches Herrania nitida var. sphenophylla, although, of course, no mention is made of the fundamentally important character of leaf-pilosity."

13. Herrania nycterodendron R. E. Schultes, Caldasia 2: 21. tt. pag. 22, 26. 1943; Bot. Mus. Leafl. Harvard Univ. 14: t. 35. 1950.
DISTRIBUTION: Westernmost parts of the Amazon Valley.

Small, slender, graceful tree up to 25 feet tall, the trunk usually simple, erect, terete, apically leafy, up to 8–9 cm. in diameter at the base, covered with an ashy-yellowish, scrobiculate bark. Leaves large, 7-digitate, stipulate, very long petiolate. Stipules caducous, linear, acute, 2.5–4 cm. long, more or less 3 mm. wide, dry, tomentose. Petiole strong, terete but very obscurely sulcate, basally slightly swollen, subferruginous, extremely densely and softly tomentose, up to about 60 cm. in length, 8–9 mm. in diameter. Leaflets sessile, unequal lanceolate-oblong, with a rather acute cusp up to 2 cm. long, basally long- and gently decurrent-attenuate, entire (or minutely and obscurely subundulate) but often very conspicuously armed with the hirsute spinule (up to 1 mm. long) formed by the prolongation of the veins; firmly chartaceous or papyraceous, the central leaflets up to 60 cm. long, 22 cm. wide, above dark green and subnitid, subglabrous or very sparsely and minutely hirsute, minutely tomentulose

along the principal veins, beneath pale green, softly stellate-pilose, very densely and softly ferruginous-tomentose along the main nerves; the veins prominently raised on both surfaces but especially so beneath. Inflorescence fasciculate, up to 40-flowered. Flowers cauline, long-pedicellate, in contracted racemes on the lower portions of the trunk. Pedicels very slender, appressed-tomentose, articulate, 2-2.5 cm. long, basally with a short, linear, apically acute bract which is densely tomentose and 3 mm. long. Bud subglobose, large, about 7-8 mm. in diameter, densely and minutely stellate-puberulent, brown. Calyx subcymbiform, divided almost to the base. Sepals 3, strongly unequal, thick, brownish-purple, valvate in the bud, externally minutely stellate-pilose, internally very minutely puberulent; the outer sepal broadly rotund-obovate, apically rotund-obtuse, entire, 19 mm. long, 15 mm. wide; the inner 2 elliptic, entire, apically subacute, about 15 mm. long, 7-8 mm. wide. Petals 5, basally sessile, widely rotund, concave, apically strongly cucullate, 10 mm. long, 8-9 mm. wide, glabrous, muricate-papillose on both surfaces but especially so on the outer, pale yellow with 7 purple nerves, ligulate. Ligules filiform, hanging, membranaceous, glabrous on both surfaces but basally minutely granulose, 2 mm. wide at base, up to 90-100 mm. long, dark purplish with prominent black nerves. Staminal tube 5-parted; stamens alternately 2- and 4antheriferous, the filaments glabrous, slender and free. Staminodes conspicuous, petaloid, reflexed, lanceolate-elliptic, acute, entire, 19-21 mm. long, 7-9 mm. wide, muricate-granulose on both surfaces. Ovary sessile, ellipsoid, 10-costate and 5-locular, densely pilose, 3 mm. long, 2 mm. in diameter, yellow. Style filiform, glabrous, apically profoundly divided into 5 parts. Stigmas 5, thick. Fruit ellipsoid, 10-12 cm. long, 4-5 cm. in diameter, apically long and gradually attenuate, often slightly constricted near the tip, apically acute or often rotund-obtuse, basally indented and pedunculate (peduncle woody, up to 4-5 cm. long, 3-4 mm. in diameter), with an extremely dense and minute velvety-stellate indumentum on all parts, without stinging hairs, very profoundly 10-costate, with 5 thick and strongly blunt-rounded primary ribs and 5 similar but smaller secondary ribs; pericarp thick-crassulent, sublignose, ashy-yellow when ripe. Seeds up to about 100, triangular or triangular-ovate in outline, flattened, 9 mm. \times 8 mm. \times 2 mm. thick, in a white pulp.

Brazil. AMAZONAS: Rio Solimões, Fonte Boa, Fróes 20578.
Colombia. AMAZONAS: Trapécio Amazónico, Río Amazonas, Leticia, Schultes 6017; interior regions of Trapécio Amazónico, between Amazon and Putumayo watersheds, alt. about 400 m., Schultes 6777; path near Quebrada Agua Negra (headwaters of Río Hamacayacu), Black & Schultes 46-389; Río Loretoyacu, Schultes 6335; Río Caqueta, La Pedrera, Anglo-Colomb. Cacao Coll. Exped. (Baker & Cope) 14, 20. CAQUETÁ: Río Caucaya, Laguna Primavera, Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 93; Río Caguán, Cartagena, Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 108; Camp Two, Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 110; Camp Three, Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 110; Camp Three, Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 113; Camp Four, Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 109; Río Caquetá, at confluence with

264 JOURNAL OF THE ARNOLD ARBORETUM [VOL. XXXIX

Río Caguán, Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 121; Camp Six, Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 128; Piedra Blanca, Anglo-Colomb. Cacao Coll. Exped. (Cope & Holliday) 131.

Peru. LORETO: Río Putumayo, Remanso, alt. 180 m., *Schultes 4011* (Type); Florida, north of Río Zubineta, alt. 200 m., *Klub 2069*; "Corbata", opposite Isla Salamanca, alt. 180 m., *Schultes 4012*; near Caucaya, *Anglo-Colomb. Cacao Coll. Exped.* (*Cope & Holliday*) 97; Río Amazonas, Mishayacu, near Iquitos, alt. 100 m., *Klug 1588*.

Herrania nycterodendron most closely resembles H. Mariae and H. Cuatrecasana. It is immediately set apart from these species, however, by its curious type of fruit. The fruit of Herrania nycterodendron has a dry, somewhat coarse and fibrous rind which is covered completely with a soft indument of velvety hairs; it lacks the stinging hairs which are usually present in this genus. The ribs of the fruit of Herrania nycterodendron are broad and rounded with deep furrows. The fruit is apically much more bluntly rounded, in most cases, than is that of related species. Fróes 20578 is a sterile collection which has been referred to Herrania nycterodendron with some reserve. The natives of the Peruvian bank of the Río Putumayo near Remanso, Isla Salamanca, refer to Herrania nycterodendron as "bat-tree" or "tree of the bats". This curious common name may be due, as several natives explained to me, to the fact that the soft, velvety indument of the fruit feels like the fur of small bats which are common in the vicinity. It may also be due to the fact that the fruits cluster on the basal portions of the stem in such a manner as to suggest bats which are accustomed to pass the day hanging from the lower parts of the trunks of small trees in the dark forests. The Witoto name, mu-se'-na, is also applied to the marraca (Theobroma glauca Karst.), and mu-sé-ge-ke, the diminutive, is very commonly used to refer to Herrania nycterodendron and possibly also to H. Mariae var. putumayonis.

14. Herrania pulcherrima Goudot, Ann. Sci. Nat. III. 2: 232. t. 5, figs. 11, 12. 1844.

Theobroma pulcherrima (Goudot) De Wildeman,⁵ Pl. Trop. Grande Cult. 89. 1902.

DISTRIBUTION: The mountainous regions of Central Colombia.

Small tree up to 15–24 feet tall, with a simple, columnar trunk 15–25 cm. in diameter. Bark thin, ashy-brown, scrobiculate, glabrous except near the apex where it is covered with a ferruginous indument. Branchlets villose, obscurely sulcate. Leaves 10–15, large, digitate, very long-petiolate, 5–7-foliate. Petioles robust, terete or sulcate, very densely ferruginous-villose, as long as the leaflets, 7–10 mm. in diameter. Leaflets sessile, unequal, lanceolate-ovate, marginally coarsely and regularly sinuate towards

⁵ This combination has been made independently by later workers, apparently unaware of the earlier publication. *Cf.* Pittier, Man. Pl. Usuales Venez. 147. 1926.

the apex, acuminate, basally attenuate, very coriaceous, mostly 45-60 cm. long (occasionally much longer), 19-35 cm. wide; above dark green, shining, coarsely muricate or minutely subtuberculate, glabrous (or extremely remotely armed with caducous hairs), the nerves minutely but densely tomentulose; beneath brownish green, densely and softly ferruginous stellate-pilose, softly and densely villose-sericeous along the veins. Stipules caducous, linear, tomentose, 3 cm. long. Inflorescence fasciculate, many-flowered (20-30). Pedicels 11 mm. long, 1.2 mm. in diameter, scabrid-hirtellous and minutely stellate-pilosiusculous. Buds ovoid, densely fulvo-tomentose, 10 \times 6 mm. Flowers large, crimson-red. Calyx subcymbiform. Sepals 3, subchartaceous, broadly ovate or elliptic-ovate, entire, rounded or subacute, externally brownish red, stellate-tomentose and stellate-puberulent, internally glabrous and crimson-red, up to 19-20 mm. long, 12-13 mm. wide, valvate in the bud. Petals 5 or (usually) 6, sessile, obovate, concave, strongly cucullate muricate-papillose or granulose on both sides, but especially externally, longitudinally striate-veined, the 5 veins prominently purple or black internally, crimson or dark red, ligulate. Ligules pendulous, 80-110 mm. long, 2-3 mm. wide, glabrous, strongly marked with 3 dark red veins, basally strongly and abruptly contracted, dark purplish red. Stamen tube 5-parted with alternately 2- and 3-antheriferous stamens and simple, short, free filaments. Staminodes very conspicuous, petaloid, lanceolate-elliptic, apically 3-fid, marginally entire, muricate-granulose on both sides, dark purple-red, 23 mm. long, 7 mm. wide. Pistil up to 7.5 mm. long. Style slender, simple yellow, 3.5 mm. long, the stigmatic tip deeply 5-fid. Ovary sessile, 5-locular, ovoid, very densely pilose, pale yellow, 4 mm. long, 3 mm. in diameter. Fruit ellipsoid, attenuate-acuminate, 10-costate, with 5 large primary and 5 smaller secondary cultriform ribs, covered, especially along the ribs, with minute stinging stellate hairs, the rind very thin when dried but crassulent in life, yellow when ripe. Seeds probably about 50, compressed, triangular in outline, in a sweet white pulp.

Colombia. META: Iraca, San Juan [de Arama], Llanos Orientales, Goudot s. n. (Type). Boyacá: region of Mount Chapon, northwest of Bogota, El Umbo region, alt. 3,000 ft., Lawrence 437. CUNDINAMARCA: Municipio de El Peñon, Hacienda "Curiche," alt. 1000 m., Jaramillo 202.

The type specimen of *Herrania pulcherrima* has always been thought to be in Paris, but, as in the case of *H. albiflora*, there is material in Geneva which may well be the true type from which Goudot's description and illustrations (at least of the flowers) were made. Goudot spoke of the type plants as inhabiting the great forests situated between the Ríos Ariari and Guayabero, affluents of the upper Orinoco, in the Colombian *llanos*. The Geneva material consists of two sheets. It is labelled in Goudot's hand, "*Herrania pulcherrima* mihi. An. Sc. Nat. 1844. Llanos del Orinoco, pueblo d'Iraca, San Juan, Flos: Dec." One sheet consists of a piece of golden-tomentose stem about one foot long, a very young leaf, and young

266 JOURNAL OF THE ARNOLD ARBORETUM [VOL. XXXIX

capsules. One of the envelopes has the native Coreguaje Indian name (reported by Goudot in the original description): "cacao cahouai — Llanos". Another envelope, on the outside of which Goudot has written "C N. 2 theobroma affinis Herrania pulcherrima," has a completely and beautifully dissected flower, the separate parts glued to the inside of the envelope. There can be no doubt but that Goudot made his drawing of the flower of Herrania pulcherrima (loc. cit. t. 5, figs. 11, 12) from this same dissection. The leaf which is preserved at Geneva could not have served as a basis for Goudot's excellent description, but a study of the material and the description would seem to indicate that the Paris material represents that from which the original description of the leaf was drawn. It may be of value to publish a few notes on Goudot's dissection of the flower. The three sepals are laid flat, the very slightly puberulent inner surface exposed. Two are rather broadly ovate, about 15 mm. long and 5 mm. wide (all measurements taken dry), apically rounded; the third, somewhat elliptic, 18 mm. long and 4 mm. wide, apically bluntly pointed. The five petals are all about equal, strongly cucullate, very densely muricate-papillose or granulose externally, papillose internally in six longitudinal lines, the ligules up to 90 mm. long, 2.5 mm. wide immediately above the constriction at its junction with the petal. The staminodes are lanceolate-elliptic, 15 mm. long, 4-4.5 mm. wide, muricate-granulose, and apically so strongly trifid that the tip appears to be mucronate. This was noted by Goudot when he described the staminodes as apically "mucronés et échancrés;" but, in his drawing, he indicated the tip as extremely acute. The ovary is very densely yellowish tomentose. It is unusual to find a species of Herrania which occurs both east and west of the Andes, as well as in the valley between the several Andean chains in Colombia. Yet that appears to be the distribution of Herrania pulcherrima. Goudot said that he had found it in the deep valleys of the eastern Andean chain, near Savana-Grande and Payme where, however, it seemed to be rare and isolated. I have seen no Goudot specimen from this locality, but it is very significant, I think, to note that all earlier and a number of the later collections were made not in the eastern llanos but within the Andean cordillera.

Vegetatively, *Herrania pulcherrima* can easily be confused (and has been confused) with *H. tomentella*, a species growing in the eastern llanos at the foothills of the Andes where the type of *H. pulcherrima* was collected. The differences between these two species are discussed under *Herrania tomentella*.

The earliest reference to *Herrania pulcherrima* is Eloy Valenzuela's minute description of the plant written in Mariquita in the Departamento del Tolima, Colombia, in 1784, while he was engaged in the work of the Mutis Botanical Expedition in New Granada. For historical reasons, this description has been reproduced in full under the generic description at the beginning of the synopsis.

In the collection of Mutis plates, there is a most strikingly beautiful and accurate water-color of a section of *Herrania pulcherrima* in full flower.

A number of diagnostic characters of this species are most clearly shown: the congested, many-flowered inflorescences, the very abbreviated pedicels, and the long and membranaceous ligules with alternate scarlet and whitish bands. Of this colored plate, there are two copies in black and white. No foliage seems to have been drawn. A search in the Mutis collection of plants in Madrid has failed to produce a specimen of *Herrania pulcherrima*. The specific name *pulcherrima*, meaning "very beautiful," could not be more appropriate. It recalls Valenzuela's picturesque remark, which I have used as a theme for this synopsis; that the flower of *Herrania pulcherrima* or *cacao esquinado* "could be considered as the greatest marvel of the plant kingdom, and one can hardly believe that nature, as frugal and simple as she is, would have used so many ribbons and so much ornamentation to adorn herself almost as ostentatiously as in the fashions".

14a. Herrania pulcherrima Goudot var. pacifica R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. 14: 131. t. 28, lower fig. 1950.

Herrania pacifica Cuatr. Rev. Acad. Col. Ciénc. Exact. Físic. Nat. 7. 27: 307. 1947. Nomen nudum.

DISTRIBUTION: Pacific coastal slope of Colombia and northern Ecuador and the Gulf of Urabá in Colombia.

A small tree up to 25 feet tall, differing from *Herrania pulcherrima* chiefly in having strongly membranaceous leaflets which are minutely stellate-pilose and not muricate or subtuberculate above; lateral leaflets usually strongly oblique; flowers which are commonly much smaller, with the petals and ligules yellow or white; and smaller fruit (11.5 cm. long, 7 cm. in diameter).

Colombia. ANTIOQUIA: north of Dabeiba, road to Turbo, Univ. Calif. 3rd Bot. Exped. Andes 1942 (Metcalf & Cuatrecasas) 30173; near Guapá, 53 km. south of Turbo, alt. about 50 m., Haught 4607; Urabá, Municipio de Mutatá, Villa Arteaga, alt. about 150 ft., Schultes & Cabrera 18707a. VALLE: Pacific Coast, Río Yurumangui, Caimanero, Cuatrecasas 16010; Río Calima, Quebrada La Brea, alt. 30-40 m., Schultes 7324. CHOCÓ: Río San Juan, vicinity of Palestina, alt. 0-30 m., Cuatrecasas 21337; Río Andaquedá, Lloro, Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 174. Ecuador. PICHINCHA: Santo Domingo de los Colorados, alt. 800 m., Acosta-Solis 10923; "foot of western cordillera", alt. 100 m., Rimbach 48.

This concept, as indicated by the varietal epithet, would seem to represent a western or Pacific coastal variant of *Herrania pulcherrima*, a species

which, in its typical form, is endemic to the Cordilleras of Colombia.

- 15. Herrania purpurea (Pitt.) R. E. Schultes, Caldasia 2: 333. 1944; Caldasia 3: 23. t. pag. 24, fig. 1, 2. 1944; Bot. Mus. Leafl. Harvard Univ. 13: 282. 1949.
 - Theobroma purpureum Pitt., Fedde Rep. Sp. Nov. 13: 319. 1914; Standl. Contr. U. S. Nat. Herb. 27: 262. t. 51. 1928; Standl., Contr. Arnold Arb.

JOURNAL OF THE ARNOLD ARBORETUM [vol. xxxix
5: 104. 1933; Standl., Field Mus. Nat. Hist. Bot. Ser. Publ. 392: 688. 1937; León, Inst. Interam. Ciénc. Agríc. Bol. Técn. 2: 6. 1949.

DISTRIBUTION: Costa Rica, Nicaragua, Panama and northwesternmost Colombia.

Small tree up to 10 feet tall, without branches along the trunk, except near the apex, with grey bark becoming glabrous but densely yellow-villose when young. Leaves usually 5-digitate, stipulate. Stipules linear, acute, dark purple, more or less stellate-villose, caducous, up to 5 cm. long, 3 mm. wide. Petioles terete, obscurely sulcate, somewhat ferruginous-villose, strong, basally rather swollen, 30-45 cm. long. Petiolules strong, very short, up to 5 mm. long. Leaflets unequal, obovate-oblong, basally cuneate, apically broadly and obtusely acuminate, entire or very obscurely sinuate, thin-chartaceous, glabrous above, sparsely and minutely stellate-villose beneath (the nerves densely stellate-villose on both surfaces), almost as long as the petioles, 22-35 cm. long, 6-13 cm. wide. Inflorescences fasciculate, 5-8-flowered. Flowers cauline, in contracted racemes on the lower and middle portions of the trunk, dark purple, pedicellate. Pedicels terete, articulate, brown-tomentose, about 4 mm. long, basally subtended by a short, linear, naviculiform bract which is densely brown-tomentose externally, glabrous internally. Buds globose, 7-9 mm. in diameter, villose. Calyx patelliform. Sepals 3 (rarely 4), united for half their length, broadly ovate or (rarely) elliptic-ovate, obtuse, entire, 12 mm. long, 9 mm. wide, brownish purple, glabrous within, ferruginous, densely stellate-tomentose without. Petals 5, sessile, obovate, strongly cucullate, up to 8 mm. (frequently less) long, 4 mm. wide, muricate-papillose on both sides but denser externally (especially along the nerves), pale purple without, veins deep purple within, longitudinally striate-nerved, 5-veined, ligulate. Ligules linear, very narrowly lanceolate, basally emarginate, acute, hanging, dark purple, about 15 mm. long, 1.8-2 mm. wide. Staminal tube 5-parted, short, 3 mm. long; stamens alternately 1- and 2-antheriferous; filaments simple, short, free; anthers about 1.5 mm. long, longitudinally dehiscent, yellow. Staminodes petaloid but not very conspicuous, ovate, apically acute, reflexed, densely muricate-granulose, red-purple, 9 mm. long, 8 mm. wide. Ovary ovoid, 10-sulcate, villose, 2.5 mm. long, 1.3 mm. in diameter. Style glabrous, 5-parted. Fruit not numerous, elliptic-ovoid, often irregularly twisted, up to 9 cm. long, 5 cm. in diameter, apically rotund-obtuse, slightly constricted near the apex, basally hardly indented, with a strong, comparatively long, peduncle, 10-costate, the 5 primary and the 5 secondary ribs almost equal, blunt-rounded, 5 mm. and 4 mm. high, respectively, and very densely armed with stinging stellate hairs, between the ribs striatefibrous and armed with stinging hairs; pericarp crassulent-coriaceous or subligneous, yellow when ripe. Seeds 25, obtusely rhomboid, flattened, about 1 cm. long, 1.3 cm. wide and up to 0.6 cm. thick.

Colombia. ANTIOQUIA: Golfo de Urabá, region around Turbo, road between Turbo and Río Grande, Schultes 5754; Río Micurí, Schultes 5755; Municipio de Pavorandocito, outskirts of Pavorandocito, alt. 80 m., Gutiérrez 2000; Mu-

SCHULTES, SYNOPSIS OF HERRANIA 269 1958]

nicipio de Mutatá, Villa Arteaga, alt. about 150 ft., Schultes & Cabrera 18653, 18593; Schultes & López 10464; Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 164, 169, 170.

Costa Rica. Palmar, Río Grande de Terraba, Pittier & Durand 3926, 6721; Pacific Coast, Boca Culebra, alt. 50 m. Pittier 12158. LIMÓN: La Colombiana Farm of United Fruit Company, alt. about 70 m., Standley 36832; Finca Montecristo, Río Reventazón, below Cairo, alt. about 25 m., Standley & Valerio 48421, 48545, 48584; Hamburg Finca, Río Reventazón, below Cairo, Standley & Valerio 48792; hills above tramline, Los Negritos Farm near Río Reventazón, Dodge & Neverman 7178. GOLFO DULCE: Playa Blanca, Valerio 461.

Nicaragua. Seemann s. n.

Panama. Monte Lirio, Hayes 398. CANAL ZONE: Near El Paraíso, alt. 30-100 m., Pittier 2574; forests along Río Indio de Gatún, Maxon 4835; Valley of Masambí, road to Las Cascadas Plantation, alt. 20-100 m., Pittier 2675; Barro Colorado Island, Gatún Lake, Maxon, Harvey & Valentine 6804, Kenoyer 443; Gatún Lake, Standley 31319; alt. 120 m., or less, Standley 40911; Armour House to second bay north, Bangham 549, Bailey & Bailey 31, Shattuck 198; near end of Fairchild Trail, Wetmore & Abbe 73; hills north of Frijoles, Standley 27434; Gamboa, Standley 28416; near Fort Randolph, Standley 28647; Obispo, Standley 31722; near Madden Dam, Alston 8861. CHIRIQUÍ: Progreso, Cooper & Slater 283. BOCAS DEL TORO: Laguna de Chiriquí and vicinity, Hart 96, von Wedel 1112; Changuinola Valley, Dunlap 448, von Wedel 976, 1721, Lucas 2. DARIEN: trail between Pinogana and Yavisa, alt. 15 m., Allen 282. PANAMÁ: vicinity of Caña, alt. 900 m., Goldman 1974; Changuinola, Cooper & Slater 12a; Changuinola and Sixaola, Rowlee & Stock 1029; Marraganti and vicinity, alt. 10-200 ft., R. S. Williams 662.

Herrania purpurea is obviously most closely allied to H. albiflora, a relationship which is discussed under H. albiflora. Both species are alone in the genus in having a curious patelliform calyx and extremely short ligules which give the flowers an entirely different appearance from those of all other species which have a subcymbiform calyx, usually with very long, filiform ligules. Herrania albiflora and H. purpurea, therefore, are considered to form a distinct section of the genus.

Further study may indicate that Her .nia purpurea might better be treated as a variety of H. albiflora; but, at the present state of our understanding, the two would seem to represent well established specific concepts which geographically are sharply delineated.

Herrania purpurea is the only species of the genus known to occur outside of South America. It has its main center of distribution in lower Middle America but it is represented in the adjacent part of Antioquia (and probably in the northern Chocó) — the northwesternmost corner of Colombia.

The binomial Herrania purpurea was published as a nomen nudum in the first edition of Thomas Belt's "The Naturalist in Nicaragua" (1874, p. 116). Belt wrote: "About here grows a cacao (Herrania purpurea) differing from the cultivated species (Theobroma Cacao)." I have been unable to discover a description of the plant or a publication of the binomial prior to 1874. In the preface of his book, Belt stated that "Prof. JOURNAL OF THE ARNOLD ARBORETUM [vol. XXXIX D. Oliver of Kew has kindly named for me some of the plants." In the collection of *Herrania* at Kew, I did not find any specimen from Nicaragua collected prior to 1874 and annotated with this binomial. Dr. N. Y. Sandwith of Kew has kindly searched through the archives and reports that he can find nothing which might suggest that Oliver had published the binomial.

Pittier's description of *Theobroma purpureum* was based upon a Panamanian collection, and he made no mention of a prior publication of this specific epithet. There is no doubt that the binomial which Belt published refers to the same concept which Pittier later and independently described and for which he used the identical specific epithet. In accordance with the International Code of Botanical Nomenclature, therefore, we must consider Pittier's *Theobroma purpureum* as the first valid use of the specific epithet.

According to Pittier (Fedde Rep. Sp. Nov. 13: 319. 1914; Standley, Field Mus. Nat. Hist. Bot. Ser. 18 (Publ. 392): 688, 1937), the Bribrí Indians of Costa Rica employ the roasted seeds for preparing a bitter drink.

16. Herrania tomentella R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. 16: 205, 213. t. 32. 1954.

Herrania nitida (Poepp.) R. E. Schultes var. aspera (Karst. & Tr. ex Tr.) R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. 14: 130. 1950, pro parte.
DISTRIBUTION: Eastern foothills of the Andes in the Orinoco drainage area of Colombia.

A small tree, slender and graceful, commonly up to 12 feet in height. Trunk erect, about 3 inches in diameter, covered with blackish bark, sparsely branched near the top or unbranched. Branches tomentose. Branchlets densely villose, with golden-rust-colored and persistent hairs. Leaves very large, digitate, 7-foliate, very long-petiolate. Petioles round, somewhat constricted at the base, very densely and softly golden or ferruginous, tomentellous, up to 60 cm. long, 9–10 mm. in diameter. Stipules persistent, linear, densely rough-tomentellous, up to 3 cm. long, 2 mm. wide. Leaflets sessile, oblanceolate or broadly lanceolate-ovate, erect, strongly unequal, membranaceous to papyraceous, acuminate, basally attenuate, the margin both regularly and lightly sinuate-dentate in the upper half but especially towards the apex and everywhere armed with cilia-like stellate hairs, 30-50 cm. long, 13-20 cm. wide, above rough to the touch with sparse, single, brown hairs, beneath rather softly and densely tomentellous with long golden-rust-colored stellate hairs. Inflorescence fasciculate, relatively few-flowered, growing from the lower portion of the trunk. Pedicels articulate, 7 mm. long, 1.5 mm. in diameter, densely stellatepilose. Buds globose, 15 mm. in diameter, densely stellate-pilose. Calyx 3-parted, divided almost to the base, subcymbiform. Sepals commonly unequal, rather carnose in life, dark purplish, strongly valvate in the bud, externally rather coarsely stellate-pilose, internally very minutely granulose-pulverulent; the 2 interior sepals round-ovate, the margins entire,

apically perfectly rounded, about 14 mm. long, 10 mm. wide; the exterior sepal usually triangular-elliptic, the margin entire, apically subacute, 13-14 mm. long, basally 6–7 mm. wide. Petals 5, basally sessile, obovate or ovate, apically very strongly concave-cucullate, about 8 mm. long, 7 mm. (often up to 8 mm.) wide, dark blood-red with purple nerves, externally minutely muricate-verrucose, ligulate. Ligules linear, about 70 mm. long, basally 3 mm. wide, filiform near the apex, dark blood-red but near the tip pinkish. Staminal tube 5-parted with stamens bearing 1 and 2 anthers alternately and with short, free filaments. Staminodes petaloid, dark blood-red, membranaceous, elliptic, marginally entire, acute, 14-15 mm. long, 6-7 mm. wide, somewhat verrucose on both surfaces. Fruits not numerous, ellipsoid, up to 9 cm. long, 4 cm. in diameter, long-attenuate but near the tip slightly constricted, the tip itself obtuse and frequently twisted, basally not indented, pedunculate, with remnants of the persistent sepals; peduncle articulate, 3 cm. long, 4 mm. in diameter, everywhere densely and very minutely velvety-pilose, soft to the touch and without stinging hairs, very deeply 10-costate, the 5 primary ribs thick and bluntly rounded, 8 mm. high, the 5 secondary ribs similar but smaller, 4–5 mm. high, transversely rather fibrous-rugose, the pericarp thick, almost woody, reported to ripen yellow. Seeds about 60, embedded in a white pulp.

A description of the pollen grain of *Herrania tomentella* is given under the generic description at the beginning of this monograph.

Colombia. [No precise locality], Rocha s. n. META: Villavicencio, alt. 300 m., Triana s. n.; Sprague 135; Sierra de la Macarena, Playa Bonita, alt. 400 m., Philipson, Idrobo & Fernández 1420; Caño Entrada, alt. 550 m., Philipson, Idrobo & Jaramillo 2199; Sabanas de San Juan de Arama, Río Guëjar, near landing-field Los Micos, alt. about 500 m., Idrobo & Schultes 612, 721; path between Río Guëjar and Caño Guapayita, alt. about 500-600 m., Idrobo & Schultes 787, 1192 (Type); Caño Yerly, Schultes 11629; Sabanas de San Juan de Arama, Río Guëjar, Schultes 11821.

Herrania tomentella resembles, in its foliage, H. pulcherrima and H. Cuatrecasana. It differs from the former in having a much more finely sinuate margin, in having a smooth (instead of a rather muricate-sub-tuberculate) upper surface, in being more finely tomentose beneath, and in being membranaceous (rather than coriaceous) and generally smaller. From the latter, it can be distinguished by differences in the shape and margin of the leaflets: those of Herrania Cuatrecasana are conspicuously long attenuate-decurrent towards the base and have very remotely and absourds even denticulate margin.

obscurely crenate-denticulate margins.

In form of the fruit, Herrania tomentella approaches H. Cuatrecasana more closely than H. pulcherrima. The capsule of Herrania pulcherrima has strongly cultriform ribs with stinging hairs, whereas that of H. tomentella has broadly rounded ribs without stinging hairs. Furthermore, floral differences between H. pulcherrima and H. tomentella are marked, especially in the staminodes which are apically trifid in the former but acute in the latter.

3

272 JOURNAL OF THE ARNOLD ARBORETUM [VOL. XXXIX

Although there are a number of resemblances between the capsule of *Herrania tomentella* and that of *H. Cuatrecasana*, the soft indumentum and lack of stinging hairs in the former are in sharp contrast to the condition in the latter where, except for stinging hairs along the ribs, the surface is glabrous or glabrescent. There are likewise several floral differences. The leaflets of *Herrania tomentella* are borne in a partly erect position. This is also true of *Herrania Cuatrecasana* and *H. pulcherrima* and possibly of all species which have a noticeably swollen callus at the base of the leaflets. In this erect position of the leaflets, *Herrania tomentella* differs

strikingly in habit from the only other species known in the Macarena, H. *nitida*, which has leaflets which tend to be rather reclinate.

A study of the fruit of the material from the Macarena has clarified a confusion of long standing. Although in the past specimens of *Herrania* tomentella have been referred to *H. pulcherrima* or to *H. nitida* (as *H. aspera* or *H. nitida* var. *aspera*), a study of the capsule, until recently unknown, shows conclusively that *H. tomentella* has its relationships in other directions. The history of the confusion between *Herrania tomentella* and *H. aspera* has been discussed in detail under the heading of *H. nitida*.

 Herrania umbratica R. E. Schultes, Caldasia 2: 261. t. pag. 263, figs. a-d. 1943; R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. 17: 86. t. 24. 1955.

DISTRIBUTION: Department of Santander, Colombia.

Small, slender, graceful tree up to about 16 feet in height, with the branches grouped at the top of the trunk. Trunk erect, up to 15-18 cm. in diameter, the bark probably brownish black; the root long, fusiform. The branchlets densely ferruginous-tomentose. Leaves very large, 7-digitate, very long-petiolate, stipulate. Stipules membranaceous, 3-6 cm. long (according to the collector). Petioles strong, sub-terete but obscurely sulcate, slightly swollen near the base, rusty, densely but softly tomentose, up to about 60–65 cm. long, basally 10 mm. and apically 4–5 mm. in diameter. Leaflets unequal, sessile, papyraceous, lanceolate-oblong, rather acutely cuspidate with a tip about 2 cm. long, basally subattenuatecuneate, entire; above dark green and almost glossy glabrous, minutely and obscurely ferruginous-tomentose along the main veins, beneath of almost the same color, very minutely and sparsely stellate-pilose, the nerves prominent and rather more densely stellate-pilose; the central leaflet 55-60 cm. (according to the collector, 40-70 cm.) long, 20-22 cm. wide; the lateral leaflets smaller. Inflorescence fasciculate, many-flowered. Flowers cauline, arising from the lower part of the trunk in abbreviated racemes, short-pedicellate. Buds globose in anthesis, 18-22 mm. in diameter. Pedicels up to 5 mm. long, densely fulvo-tomentose, articulated basally and subtended by a minute, linear bract. Buds globose, mostly 10-12 mm. in diameter. Calyx patelliform, obscurely 2-parted. Sepals very fleshy, 2, connate most of their length, subequal, rotund-ovate, entire, apically rounded, more or less 22 mm. long, 22 mm. wide, glabrous and

purple within, without yellow-brown and very densely and minutely stellatepilose and sparsely and coarsely stellate pilose. Petals 5, sessile, thick, blood-red, concave, obovate, mostly 9 mm. long, 8 mm. wide, apically stongly cucullate, within with 5 thick-callused, purple, muricate-papillose veins, glabrous between the nerves but near the thickened margin densely muricate-papillose. Ligules linear, 19 mm. long, 2 mm. wide at base, the base strongly and abruptly contracted, spirally twisted in the bud but in flower erect, yellowish red, minutely granulose. Staminal tube 5-parted, the stamens 2- and 4-antheriferous, with short, free, strongly flattened filaments; anthers 2-locular, the locules 1.5 mm. long, 0.6 mm. wide, yellow. Staminodia thick, conspicuously petaloid, yellowish, strongly deflexed, hiding the petals and anthers, oblanceolate-elliptic, entire, apically subacute, 20 mm. long, 10 mm. wide, densely papillose-granular on both surfaces. Ovary sessile, elongate-ovoid, 10-costate and 5-locular, reddish golden, very densely stellate-pilose, 3 mm. in diameter. Style fleshy-terete, simple, yellow, apically conspicuously 5-parted into a stigma, 1 mm. long. Fruits numerous, up to 45 to a tree; elongate-ellipsoid, conspicuously irregular, mostly 11-14.5 cm. (according to the collector, up to 17 cm.) long, 4.5-5 cm. (according to the collector up to 8 cm.) in diameter, apically rotund-obtuse, not constricted near the apex, basally obtuse (not indented) and pedunculate (with a woody, articulated peduncle up to 10 mm. long, 4 mm. in diameter), with 10 subequal ribs, the 5 primary ribs thick, irregular, blunt-rounded, 6-8 mm. high, 5 mm. wide, the secondary ones similar but rather smaller, about 5 mm. high, 5 mm. wide, somewhat striate-fibrous between the ribs, very sparsely and rather grossly beset with simple, white, probably stinging hairs up to 1.5 mm. long, lacking a velvety indumentum; pericarp crassulent-leathery or subligneous, 3-4 mm. thick; bright yellow when ripe. Seeds 45, triangular or angular-ovate in outline, flattened, 13 mm. \times 10 mm. \times 3 mm., in a white pulp, measuring 18 mm. \times 15 mm. \times 7 mm. with the pulp.

Colombia. SANTANDER: Municipio de Girón, region of Capitancitos, alt. 695 m., Ortíz Méndez s. n. (Type). NORTE DE SANTANDER: Río Tibú, above Beltrania, Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 179; Río Orú, Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 180; Río Nuevo, Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 182; Río Nuevo, Anglo-Colomb. Cacao Coll. Exped. (Bartley & Holliday) 182. Trinidad. Imperial College of Tropical Agriculture, Baker s. n.

When Herrania umbratica was originally described, the resemblance of its fruit to that of H. nycterodendron led to the suspicion of some relationship between the two concepts. Further investigation, however, has indicated that Herrania umbratica and H. albiflora are probably very closely allied. The vegetative differences between Herrania umbratica and H. albiflora are slight. Herrania albiflora f. titanica would seem to represent, in some respects, a link between the two species. Exact relationship, however, cannot be established, until complete flowers of Herrania umbratica and additional fruits of H. albiflora are found. In the present state of our 274 JOURNAL OF THE ARNOLD ARBORETUM [VOL. XXXIX

knowledge, we may say that the fruit of Herrania umbratica, similar in some respects to that of H. nycterodendron, differs from the fruit of H. albiflora (as represented in Goudot's line drawing published with the original description of H. albiflora and as known for H. albiflora f. titanica) in being irregularly contorted (instead of very regular); in having the primary and secondary ribs nearly equal and so thick that there is little flat intercostate area (instead of having the primary ribs twice or more higher and much thicker than the secondaries and extensive flat areas between the ribs); in being apically extremely thick and blunt (instead of having a slender, somewhat attenuate tip which is but slightly obtuse); and in having the peduncle much stouter than that of H. albiflora. Further investigation and additional collections may possibly indicate that Herrania umbratica would better be considered as a variety of H. albiflora, but a complete understanding of the floral structure of H. umbratica must be had before any definite decisions can be made in this respect. The collector of the type of Herrania umbratica records that this same species is found in townships in the vicinity of Girón, the type locality: San Vicente, Lebrija, Zapatoca, and Betulia. There are, however, no specimens from these localities. Regarding the habitat of Herrania umbratica, Ortíz Méndez wrote in his field notes: ". . . loose sandy, sandyclay soils . . . the normal growth of the plant occurs in rather wet situations . . . it grows and develops in the shade of the trees which are known in the region by the names juanblanco, canalete, guarumo, guamo, anaco, barba de mono, cocotinajo, qualanday, etc." Of diseases which attack Herrania umbratica, he reported: "The trunk and branches are completely healthy. There are sporadic cases of insect attack to the fruits, but these attacks do not harm the seeds. Fungal attack is absolutely negative. The leaves are attacked slightly by crisomélidos and minadores."

PLANTS OF UNCERTAIN POSITION

Тнеовкома Mariae (Mart.) K. Schum. f. MINOR Diels, Notizbl. 15: 48. 1940. The possible position of this concept is discussed under *Herrania nitida* f. *sphenophylla*.

THEOBROMA MONTANA Goudot ex Bernoulli, Neue Denkschr. allg. Schweiz. Gesell. gesam. Naturw. 24: 15. 1871, nomen nudum. Under the caption: "species mihi ignotae," Bernoulli published this name without a description and without the citation of specimens. It may represent a species of *Herrania*, for Bernoulli commented: "Vero similiter *Herraniae* species."

HERRANIA GUIANENSIS Sagot ex K. Schum. Mart. Fl. Bras. 12(3): 75. 1886. Nomen in syn. French Guiana. "Karouany", Sagot (?) s. n. When K. Schumann published as a synonym of *Theobroma speciosum* Willd. ex Spreng. Sagot's manuscript name *Herrania guianensis*, he cited Sagot 1206, a collection from French Guiana consisting merely of flowers. In the Utrecht herbarium, I found specimen number 000030 to be a collection of flowers only. They represent *Theobroma speciosum*, but on the outside of the packet there is a handwritten 1958]SCHULTES, SYNOPSIS OF HERRANIA275annotation: "Herrania guianensis Sagot". This is probably part of the Sagot
collection cited by Schumann.275

COMMON AND NATIVE NAMES KNOWN FOR THE SPECIES OF HERRANIA

In compiling the following enumeration of names used for *Herrania* in Middle and South America, I have included all orthographical variants which have been found in the literature. The list is made up from the literature, from labels on herbarium specimens and from my own ethnobotanical observations in the field. In each case, the country or countries in which the name is employed has been indicated. Some of the names reported are taken from the Indian languages, in which cases it has almost always been possible to designate the specific tribe.

abare a-no-kwa a-wa-ka-de-ro awarivacabariyek bee-ay-o be-se-o-wa boscacao bur-oo-ma

cacahuillo cacahuio cacaíta cacao cahouai cacao cahouit cacao cahousi cacao caimán cacao canaludo cacao cimarrón cacao cuadrado cacao de andirá cacao de ardilla cacao de chimbe cacao de cintillas cacao de macaco cacao de mico

Venezuela: (Musuchíes Indians) H. lemniscata Colombia: (Kubeo Indians) H. nitida Colombia: (Kuripako Indians) H. nitida H. lemniscata Venezuela Colombia: (Makuna Indians) H. nitida H. nitida Colombia (Tanimuka Indians) H. kanukuensis Dutch Guiana British Guiana: (Arawak H. lemniscata Indians) H. nitida Perú H. nitida f. sphenophylla Perú H. albiflora Venezuela H. pulcherrima Colombia H. pulcherrima Colombia H. pulcherrima Colombia Colombia Colombia, Ecuador H. purpurea Costa Rica Colombia Brazil H. purpurea Panamá Colombia, Perú Colombia Brazil Costa Rica H. purpurea Colombia H. Mariae Brazil Colombia

cacao de monte

Ecuador

H. Mariae, H. nitida H. Cuatrecasana H. pulcherrima H. Mariae var. putumayonis H. nycterodendron H. laciniifolia H. Camargoana H. Camargoana H. albiflora & f. titanica, H. breviligulata, H. Cuatrecasana, H. Dugandii, H. laciniifolia, H. Mariae, H. nycterodendron, H. tomentella H. balaensis, H. pulcherrima var. pacifica H. purpurea H. nitida, H. nycterodendron H. nycterodendron H. pulcherrima H. purpurea H. albiflora H. albiflora H. Camargoana, H. Mariae, H. Mariae var. putumayonis

cacao de murcielago cacao esquinado cacao maní cacao montarás cacao montaráz cacao jacaré Panamá Perú Colombia, Perú Colombia Panama Colombia Brazil

JOURNAL OF THE ARNOLD ARBORETUM VOL. XXXIX

cacao quadrado cacao silvestre

276

cacao simarrón cacao symarrón cacaoito de monte cacaorana caca-ú cacau de quina cacaui cacau-jacaré cacau-rana cahouit cha-te-ra

Brazil Colombia Colombia

Perú Colombia Colombia Colombia Brazil Brazil Brazil Brazil Brazil Brazil Colombia Colombia, Perú: (Tikuna Indians) Panamá Panamá Brazil: (Tukano Indians) Colombia: (Yukuna Indians)

H. Mariae H. pulcherrima H. laciniifolia, H. Mariae var. putumayonis, H. nitida H. nitida, H. nycterodendron H. albiflora H. albifloraH. nitida, H. pulcherrima H. Mariae H. Mariae H. nycterodendron H. Mariae H. Mariae H. Mariae H. pulcherrima H. nitida

chocolatillo coco del monte ee-so-pe-ke hee-ree-la-na-peeta-re he-me-ka-ra jo-kee-kee-yo-ke ko-kee-ot-chu

ku-ra-ta maipoilie doron doron ma-mi-ree

Colombia: (Taiwano Indians) Colombia: (Kubeo Indians) Colombia, Ecuador: (Kofán Indians)

Colombia: (Karijona Indians) H. nitida Dutch Guiana: (Karib Indians) H. kanukuensis

Colombia: (Kabuyari Indians) H. nitida Dutch Guiana: (Karib Indians) H. kanukuensis H. lemniscata Venezuela: (Maquiritare Indians) Colombia: (Karijona Indians) Colombia, Perú: (Witoto Indians) Colombia, Perú: (Witoto Indians) Brazil: (Tukano Indians) Colombia: (Desano Indians) Colombia, Perú Colombia, Perú Colombia Panamá: (Bribrí Indians) Colombia: (Inga Indians)

H. purpurea H. purpurea H. Camargoana H. nitida

H. nitida H. nitida H. Cuatrecasana, H. nitida

maripoele kakaoeleo matayaka

mi-to-ro-re mu-se-ge-ke

mu-se-na

o-so-pee-ko o-yaw-pee-ka-ye palo de chimbe palo de murciélago pan y cacao rus-ub sacha cacao

so-pee-ja-ke tach-ko-au toot-choo wild cacao wild cacao

Colombia: (Gwanano Indians) Colombia: (Miraña Indians) H. nitida Colombia: (Yurutí Indians) Panamá: Canal Zone British Guiana

H. nitida H. Mariae var. putumayonis, H. nycterodendron H. Mariae var. putumayonis, H. nycterodendron H. Camargoana H. nitida H. nycterodendron H. nycterodendron H. albiflora H. purpurea H. breviligulata, H. Cuatrecasana H. nitida

H. nitida H. purpurea H. lemniscata

INDEX TO EXSICCATAE

For purposes of facility in consulting material of *Herrania* in our herbaria, the following list summarizing the collections which have been consulted in the preparation of this synopsis is offered. The list is arranged alphabetically by the last name of the collector. Numbers in parentheses refer to the corresponding species in the text.

Acosta-Solis 10923 (14a) Allen 282 (15) Alston 8861 (15) André K 26 (2) Kalbreyer 2047 (9) Kenoyer 443 (15) Killip 34247 (12) Killip & Smith 27431, 28234 (12)

Anglo-Colombian Cacao Collecting Expedition 78 (3); 35, 39, 45, 56 (4); 80, 84, 86 (5); 89 (8); 55c, 67, 76, 85, 87, 88, 92, 100, 106, 112, 120 (12); 93, 108, 109, 110, 128, 131 (13); 174 (14a); 164, 169, 170 (15); 179, 180, 182 (17). Archer 2514 (10) Aristeguieta 1598 (1) Bailey s.n.(1)Bailey & Bailey 31 (15) Bangham 549 (15) Bates s.n. (16) Black 47–1916 (11) Black & Schultes 46-223 (11); 46-331 (12a); 46-389 (13)Bonpland 1580 (1) Cooper & Slater 12a, 283 (15) Cruz (de la) 3892 (10) Cuatrecasas 11168 (5); 10742 (6); 16010, 21337 (14a) Curran 135 (1) Dodge & Nevermann 7178 (15) Ducke 595 (11); s.n., 7618 (12) Dunlap 448 (15) Eggers 14362 (2) Exped. Bot. Mutisii Novae-Granat. 3759 (1); 937 (9)Forest Dept. British Guiana F 1764 (10) Fróes 21468, 21540, 22673 (3); 23003 (7); 20630, 21041 (11); 20919 (12); 21040 (12a); 20578 (?13)García-Barriga 8375 (9), 14016 (12) Ginzberger 804 (11) Glaziou 9635 (12) Goldman 1974 (15) Gonggrijp 2111, 2565, 4101, 4117, 4126 (7)Goudot s.n. (1); s.n. (9); s.n. (14) Grassl 10121 (12) Hart 96 (15) Haught 1490 (1a) Hayes 398, 399 (15) Hulk 26 (7) Idrobo & Schultes 768, 791, 1325 (12); 612, 721, 787, 1192 (16) Im Thurn s.n. (10) Jaramillo 202 (14)

Klug 1853 (12a); 1588, 2069 (13) Krukoff's 4th Exped. Bras. Amazon 4523 (11)Krukoff's 5th Exped. Bras. Amazon 6085 (12×11) Lanjouw & Lindeman 2304 (7) Lawrence 437 (14) Lucas 2 (15) von Martius s.n. (11) Martyn 61 (10) Maxon 4835 (15) Maxon, Harvey & Valentine 6804 (15) Mexía 7328 (3) Murça Pires 775, 1159 (4) Murça Pires & Black 740 (11); 873 (12) Myers 3371 (10) Ortíz Méndez s.n. (17) Pennell 3799, 3832, 4208 (1) Pérez-Arbeláez 10303 (9) Philipson et al 1420, 2199 (16) Pittier 2574, 2675, 12158 (15) Pittier & Durand 3926, 6721 (15) Poeppig 1979 (12) Purdie s.n.(1)Richter s.n. (1a) Rimbach 48 (14a) Rocha s.n. (16) Rowlee & Stork 1029 (15) Ruíz & Pavón (?) s.n. (12) Rusby & Squires 252 (10) Schomburgk s.n. (10) Schultes 18639 (1); 18638 (2); 3342 (5); 6038 (6); 3478, 3670 (8); 6238, 6461, 6759, 8072 (11); 4010 (11a); 3405, 3698, 3730, 5351, 5359, 5491, 5529, 5685, 5715, 5850, 5876, 6000, 6016, 6054, 6058, 6118, 6124, 6141, 6142, 6143, 6144, 6145, 6146, 6147, 6149, 6192a, 6304, 6383, 6640, 6878, 8129, 11627 (12); 4011, 4012, 6017, 6335, 6777 (13); 7324 (14a); 5754, 5755 (15); 11629, 11821 16). Schultes, Baker & Cabrera 18439, 18553 (12)Schultes & Black 8286, 8377 (12) Schultes & Cabrera 18720, 19082 (3); 18712, 18715, 18976, 19100 (5); 13628,

JOURNAL OF THE ARNOLD ARBORETUM [VOL. XXXIX

13630, 13632, 14343, 14537, 14880, 14882, 18933, 19284, 19665 (12); 18707a (14a); 18652, 18693 (12)

278

Schultes & López 8758, 8759, 8762, 8763, 8956, 9144, 9162, 9205, 9240, 9416b, 9619, 9722, 9747, 9869 (4); 10464 (15).
Schultes & Murça Pires 8978, 9130 (4)
Schultes & Smith 2050 (3)

Schunke 45 (12a) Scolnik, Araque Molina & Barkley 195001 Standley & Valerio 48421, 48545, 48584, 48792 (15)
Steyermark 60558 (10)
Tejera 268 (1)
Tessmann 4024 (12); 3287 (12a)
Traill 64 (12); 65 (11a)
Triana s.n., 5333, s.n. (12)
Ule 5031 (11)
Univ. Calif. 3rd Bot. Gard. Exped. Andes 30173 (14a)
Valerio 461 (15)

(10)
Seemann s.n. (15)
Shattuck 198 (15)
Smith 3541 (7)
Sprague 135 (16)
Spruce 4969 (12)
Stahel & Gonggrijp 3015 (7)
Standley 27434, 28416, 28647, 31319, 31722, 36832, 40911 (15)

Wetmore & Abbe 73 (15)
L. Williams 11339 (10); 2332, 2816, 2843, 3345, 3364 (12)
R. S. Williams 662 (15)
Collector unknown [Hort. Trinidad] s.n. (1)

Von Wedel 976, 1112, 1721 (15)

BOTANICAL MUSEUM HARVARD UNIVERSITY



PLATE I

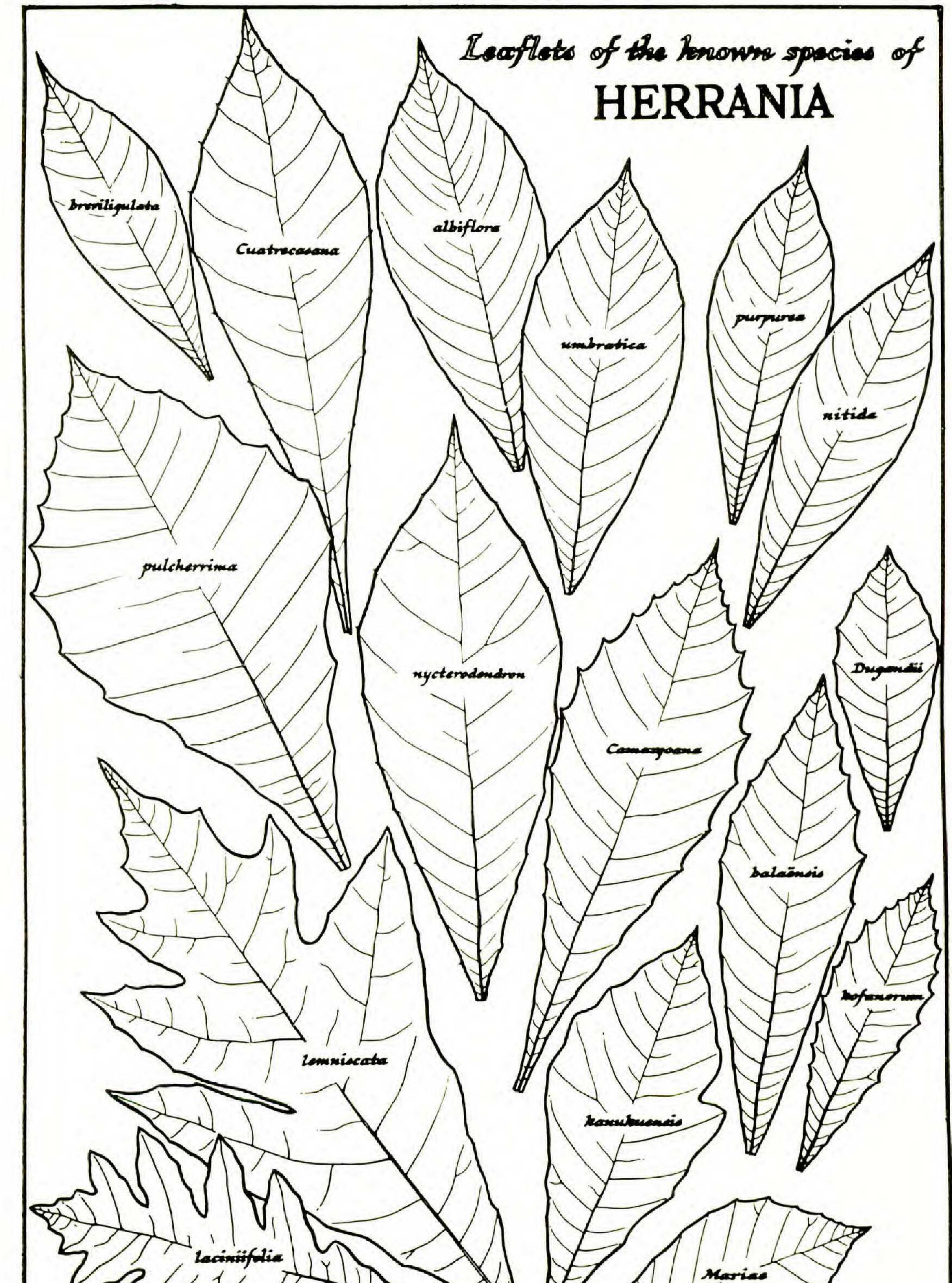
la episemin menus m. pensio- niculara. y alge levantada conserve et prussera vender debys del épissenmi, y flexibilisionar de insenios blanco, fibros, lipero, y en el corre hanversal se vé radio. con mias q' han al mester de la mima contera : este el blan. quisime béfo, y cereate & orificios capillar. p? donte mana in juso mui caitalino y gelannoso CEPTER OF D BREED, SWEED, SWEED, SWEED, STOR Mas: grander, alternas, upion & pelo ahue, Ipanio, autarel mismo peron comun = Veron: comune por enter, praler, mulcisularos alo lango, y peniculados enlos extremos = . Opielas: cumeifonon conta mirad infinion, Escabras p. cnuma, mentramecers, y & boxes inkan aropador de prentar Tippousculais la mayor remede al posso comun : las interior, chicai, obroaro oblongas, obtuias dans fa : las environ. Je enviranchan desde la mirad, y abren en laumas primadas, anchas, acuminadas, delas q don mas grandes las and any marking the marked and Monenas; mas anchas las 3 terminales. En alyun. ojas

1. 6 4 4 1 de suele anadia una chica y zome antes delas primezas= Venas: paralelas, rectas, de frant. = Cutip. dos Il las enifolias, algo Distantes dela amilia, Jubuladas, adminiai, pol-lican. y conform love al ensenon del tallos A lon! Mor: amonionadas anoidas, asil·las. y supraavil las enla panie informe del tallo, y cari impre enla assillar der. midas, pot-lican. ligenam. Olonosas, y & colon purpures, obien a cannin profunso. = l'edunc. ming. = Vedic. Semullos, levantad. delpadrios p? el prie y con 2 0 3 blas Jubulas contras

Calipenianche monogohyllo, coniaceo, colonido, peludo es ren-onné: antes de abrin es cennado, obrado, obraso: no se dunde

Page of manuscript of Valenzuela's Diario de la Expedición Botánica al Reino de Nueva Granada in which the detailed description of cacao esquinado (Herrania pulcherrima) is set down.

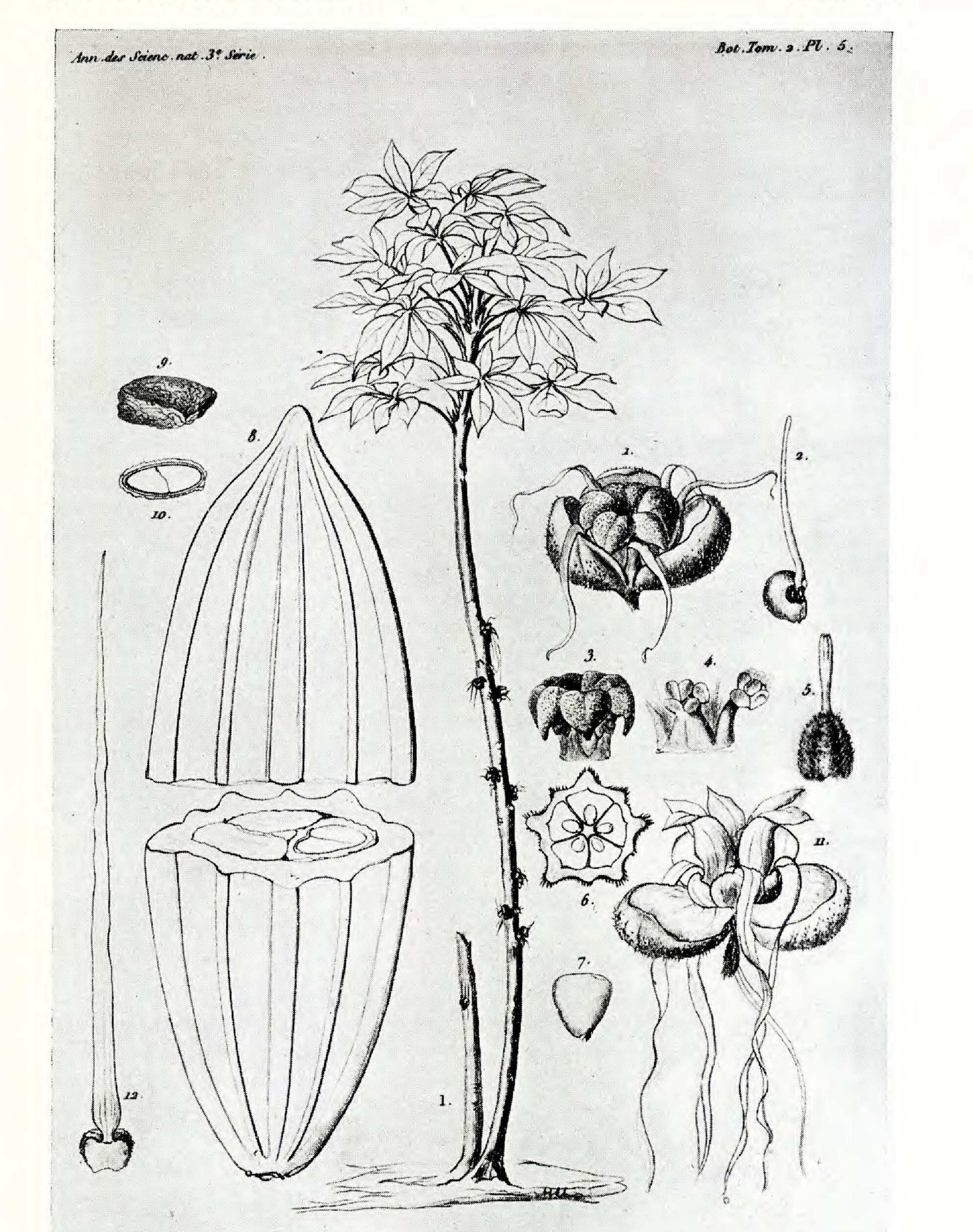
PLATE II



Ew.Smith

Forms of the leaflets of sundry species of Herrania.

PLATE III



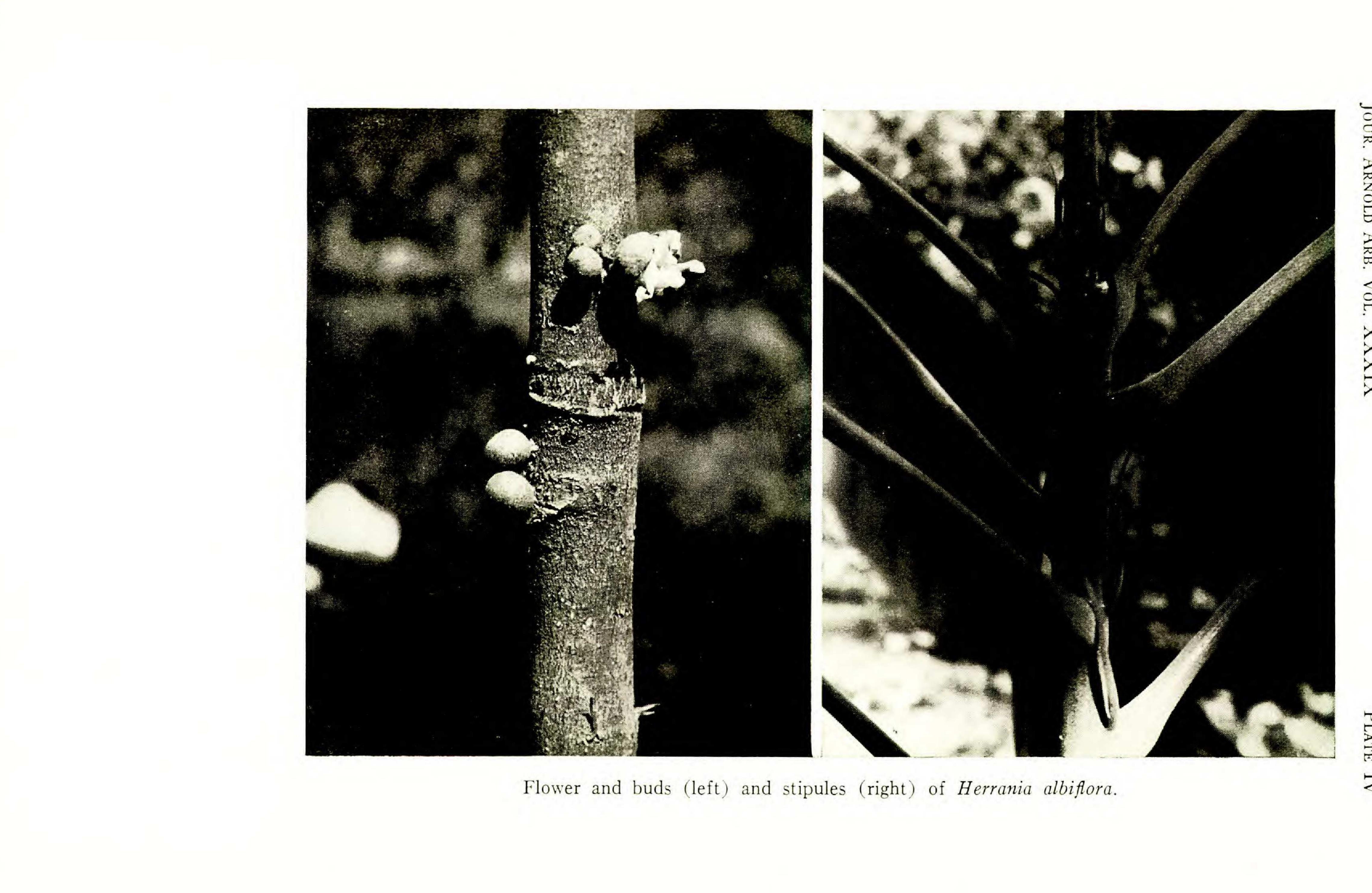
J Goudot del.

M. Douliot se

juin à 1

1. Herrania albiflora Gdt

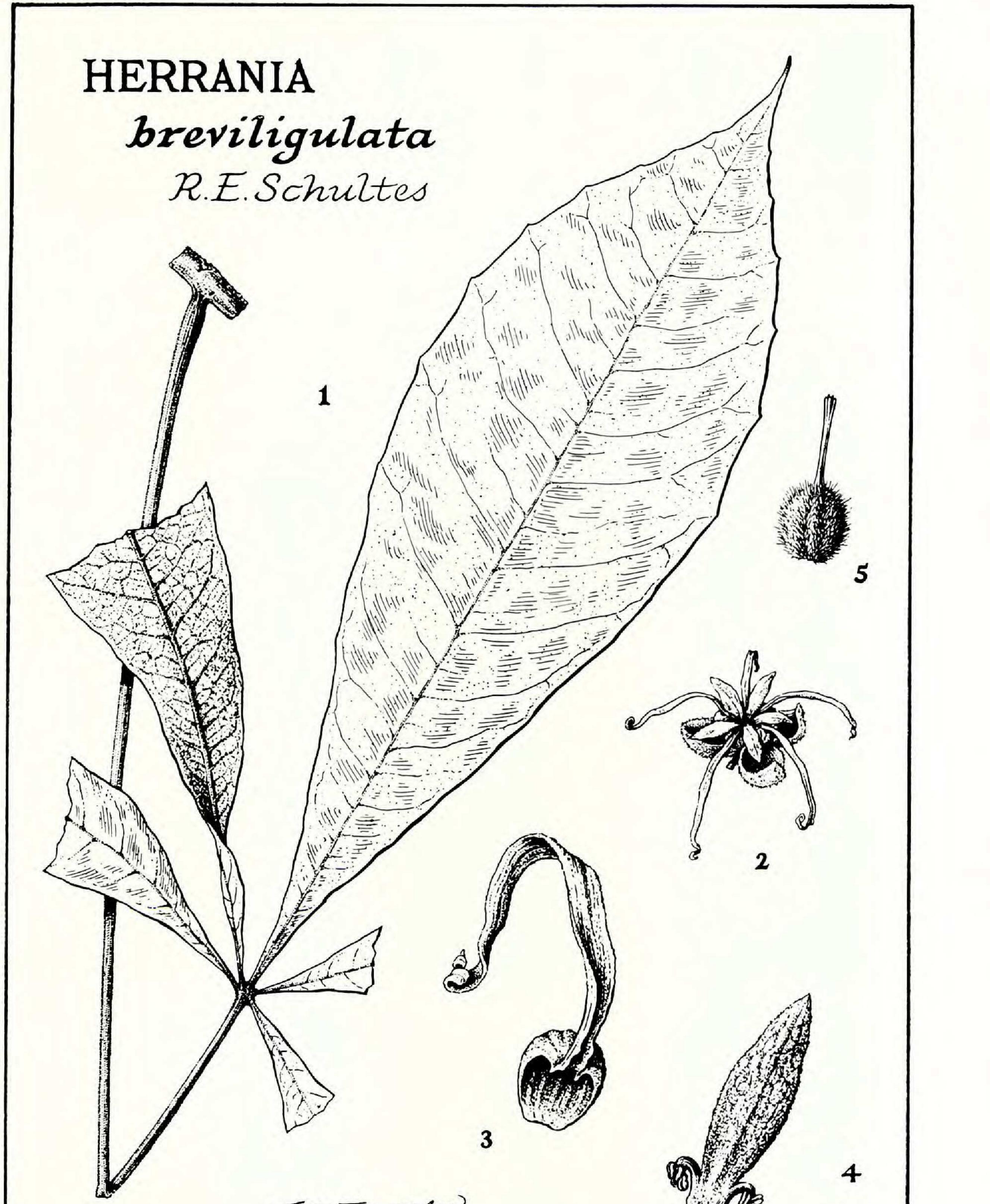
Drawing of *Herrania albiflora* from Goudot's original description of the genus and species.



PL ATE IV

C R R 11 -10 D RB XIX

Plate V



Ew.Smith)

Herrania breviligulata. FIG. 1. Leaf, $\times 1/3$. FIG. 2. Flower, $\times 1/2$. FIG. 3. Petal, $\times 2$. FIG. 4. Staminode and anthers, $\times 2$. FIG. 5. Ovary and style, $\times 4$.

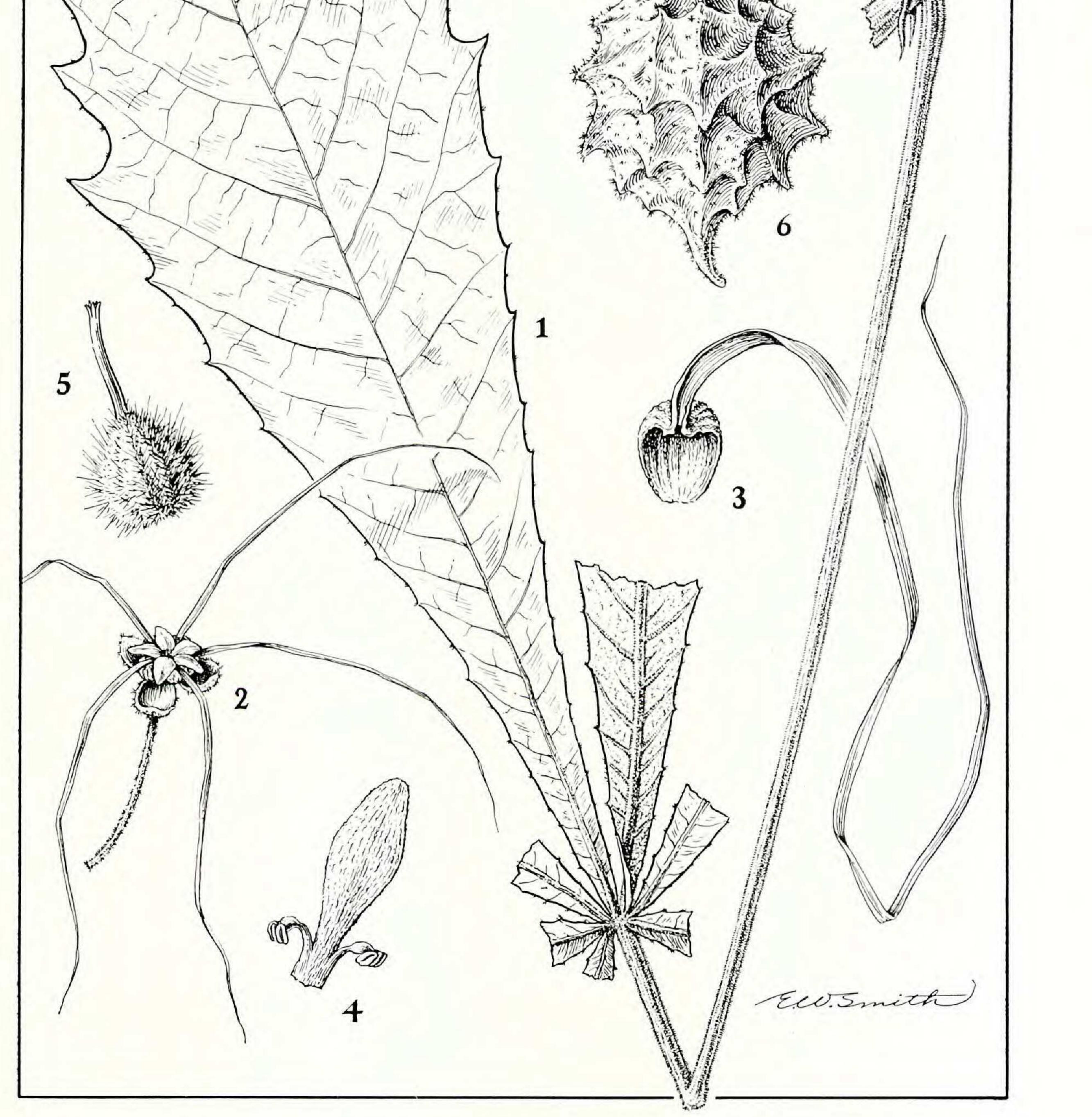
Plate VI



Fruits of Herrania breviligulata.

FLATE VII

HERRANIA Camargoana R.E.Schultes



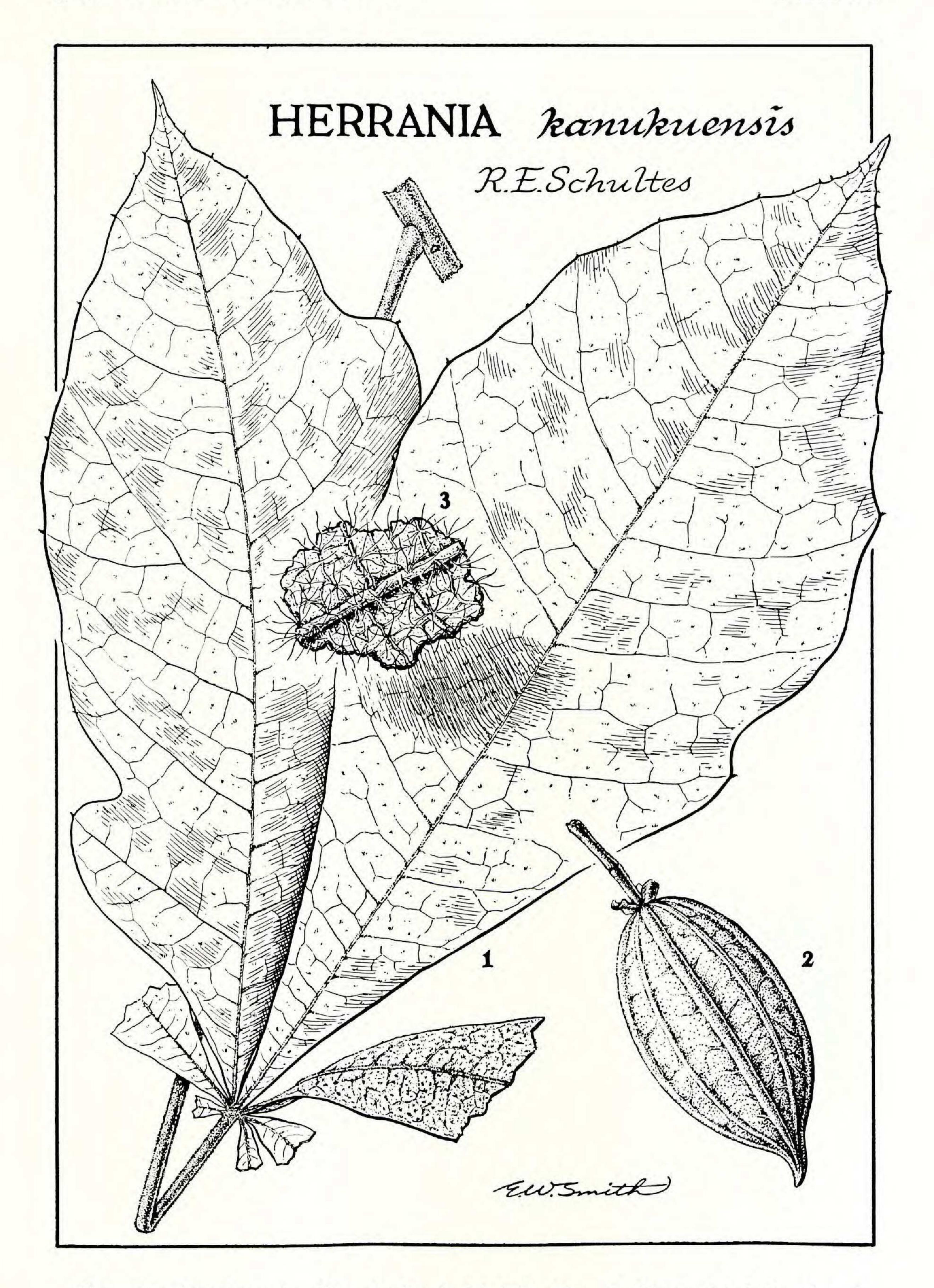
Herrania Camargoana. FIG. 1. Leaf, $\times 1/4$. FIG. 2. Flower, $\times 1/2$. FIG. 3. Petal, $\times 2$. FIG. 4. Staminode and anthers, $\times 2$. FIG. 5. Ovary and style, $\times 4$. FIG. 6. Fruit, $\times 1/2$.

Plate VIII



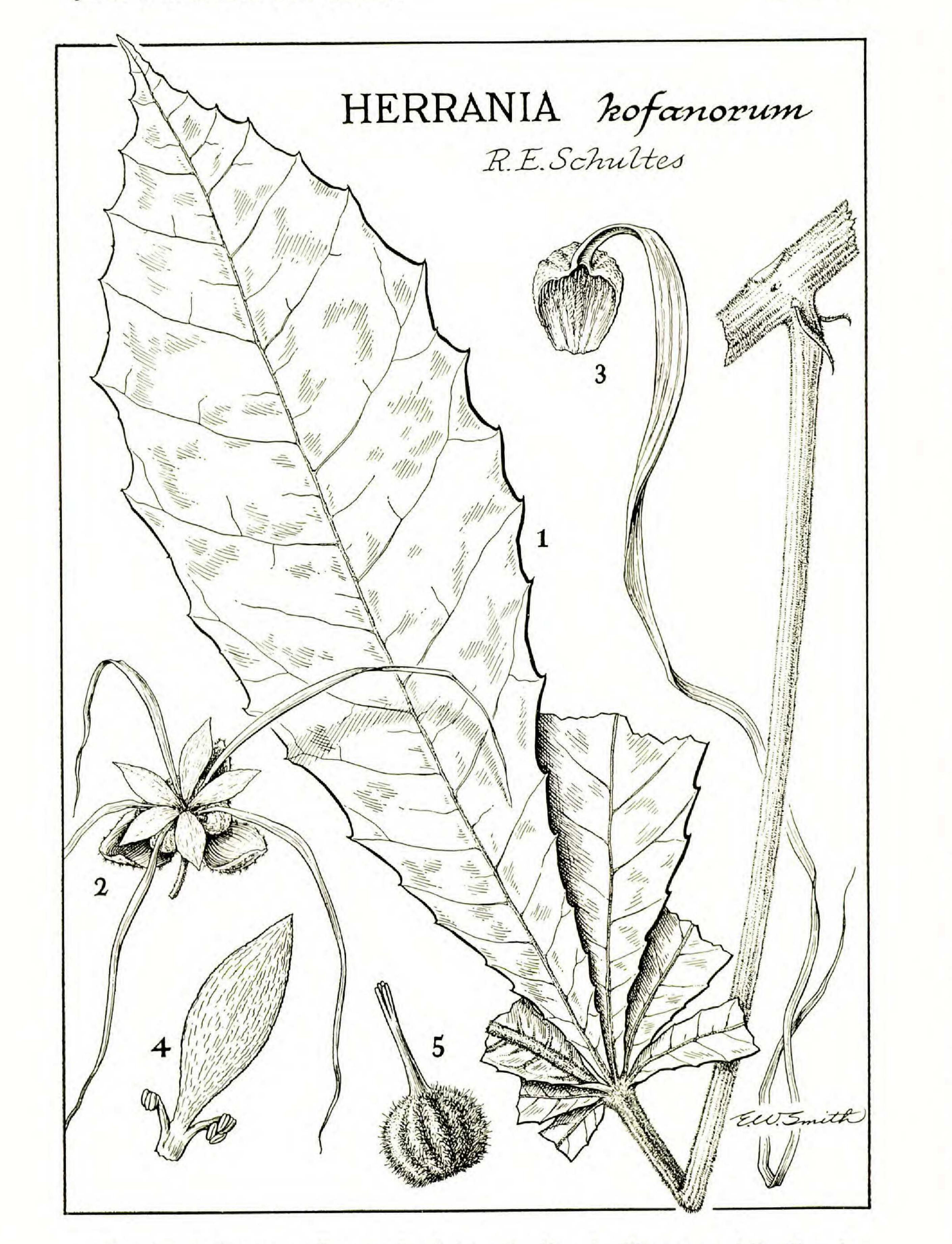
Inflorescences of Herrania Camargoana.

PLATE IX



Herrania kanukuensis. FIG. 1. Leaf, \times 1/6. FIG. 2. Fruit, \times 1/2. FIG. 3. Portion of lower surface of leaflet, showing pilosity, \times 4.

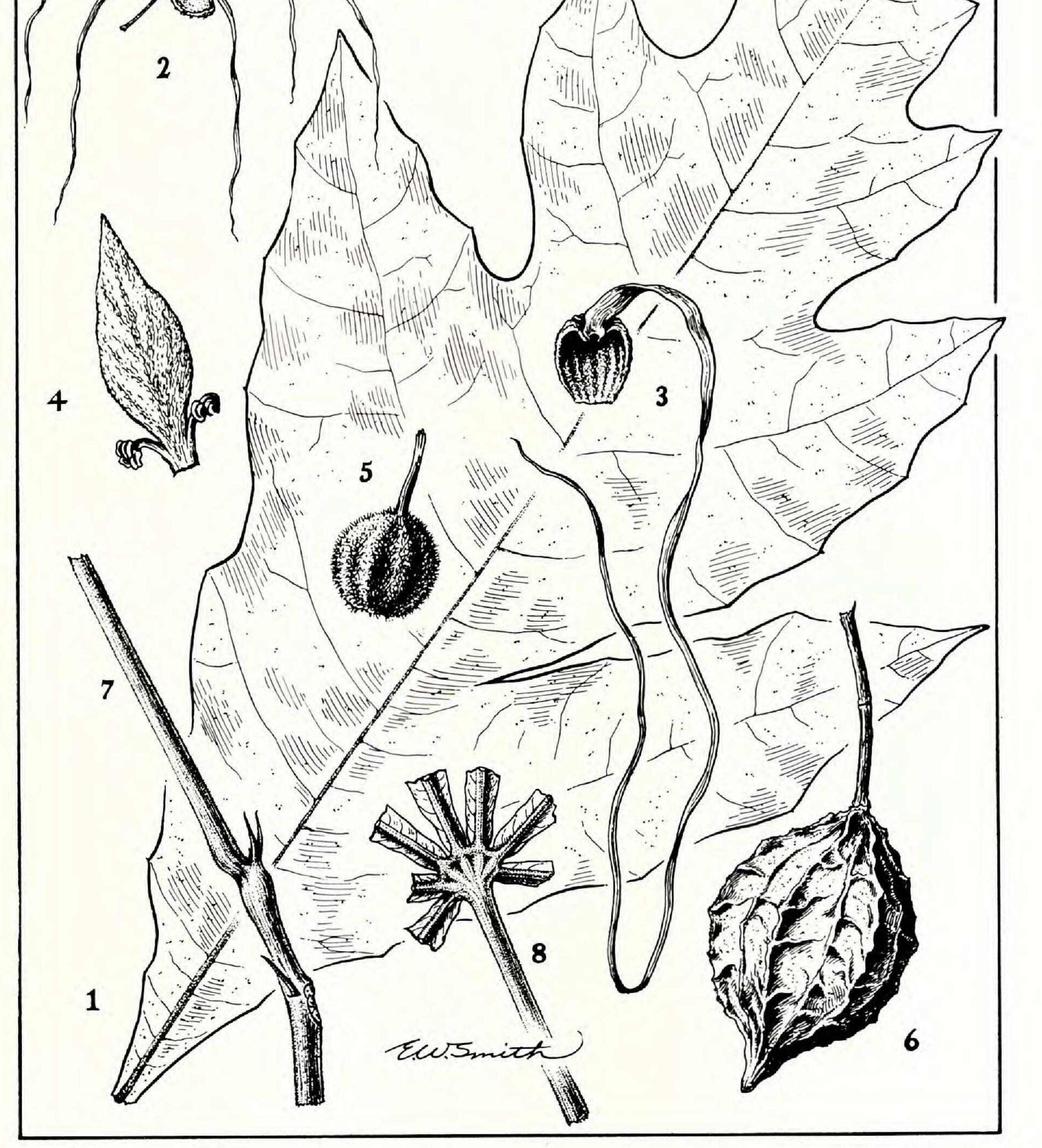
PLATE X



Herrania kofanorum. FIG. 1. Leaf, $\times 1/2$. FIG. 2. Flower, $\times 1/2$. FIG. 3. Petal, $\times 2$. FIG. 4. Staminode and anthers, $\times 2$. FIG. 5. Ovary and style, $\times 4$.

PLATE XI

HERRANIA lemniscata (Schomburgk) R.E. Schultes



Herrania lemniscata. FIG. 1. Leaflet, $\times 1/5$. FIG. 2. Flower, $\times 1/3$. FIG. 3. Petal, $\times 2$. FIG. 4. Staminode and anthers, $\times 2$. FIG. 5. Ovary, $\times 2$. FIG. 6. Fruit, $\times 1/2$. FIG. 7. Petioles and stipules. FIG. 8. Base of leaflets.

PLATE XII



Herrania lemniscata. Schomburgk's field painting of Lightia lemniscata, Tab. XLI in the Schomburgk collection of water-colors in the British Museum (Natural History).

Jour. Arnold Arb. Vol. XXXIX

PLATE XIII



Flowers and buds of Herrania Mariae var. putumayonis.

PLATE XIV



Fruits of Herrania nitida.

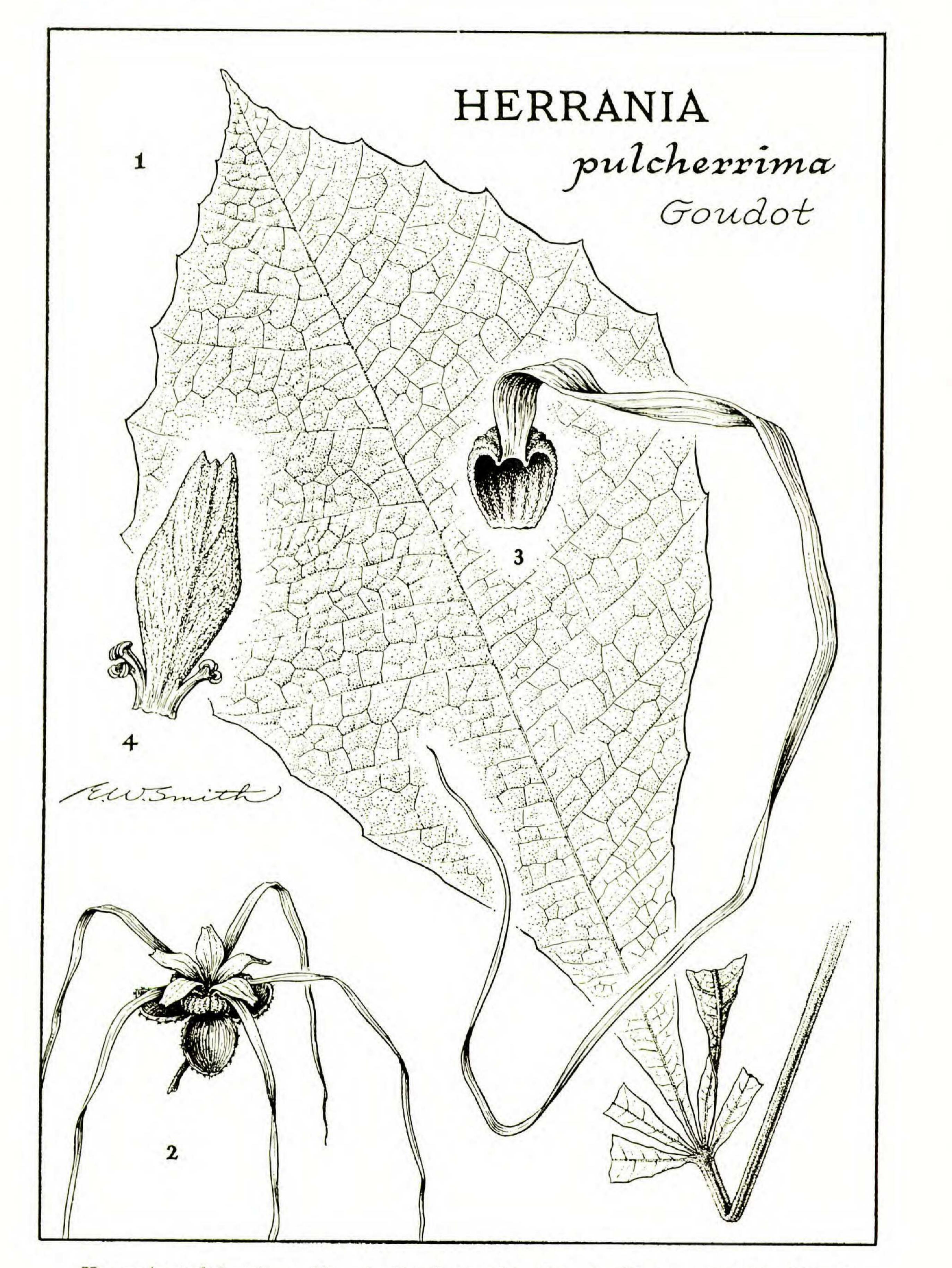
PLATE XV



Ew.Smith

Herrania nycterodendron. FIG. 1. Leaf, $\times 1/4$. FIG. 2. Flower, $\times 1/2$. FIG. 3. Staminode and anthers, $\times 2$. FIG. 4. Ovary and style, $\times 4$. FIG. 5. Fruit, $\times 1/2$. FIG. 6. Portion of lower surface of leaf, showing pilosity, $\times 4$.

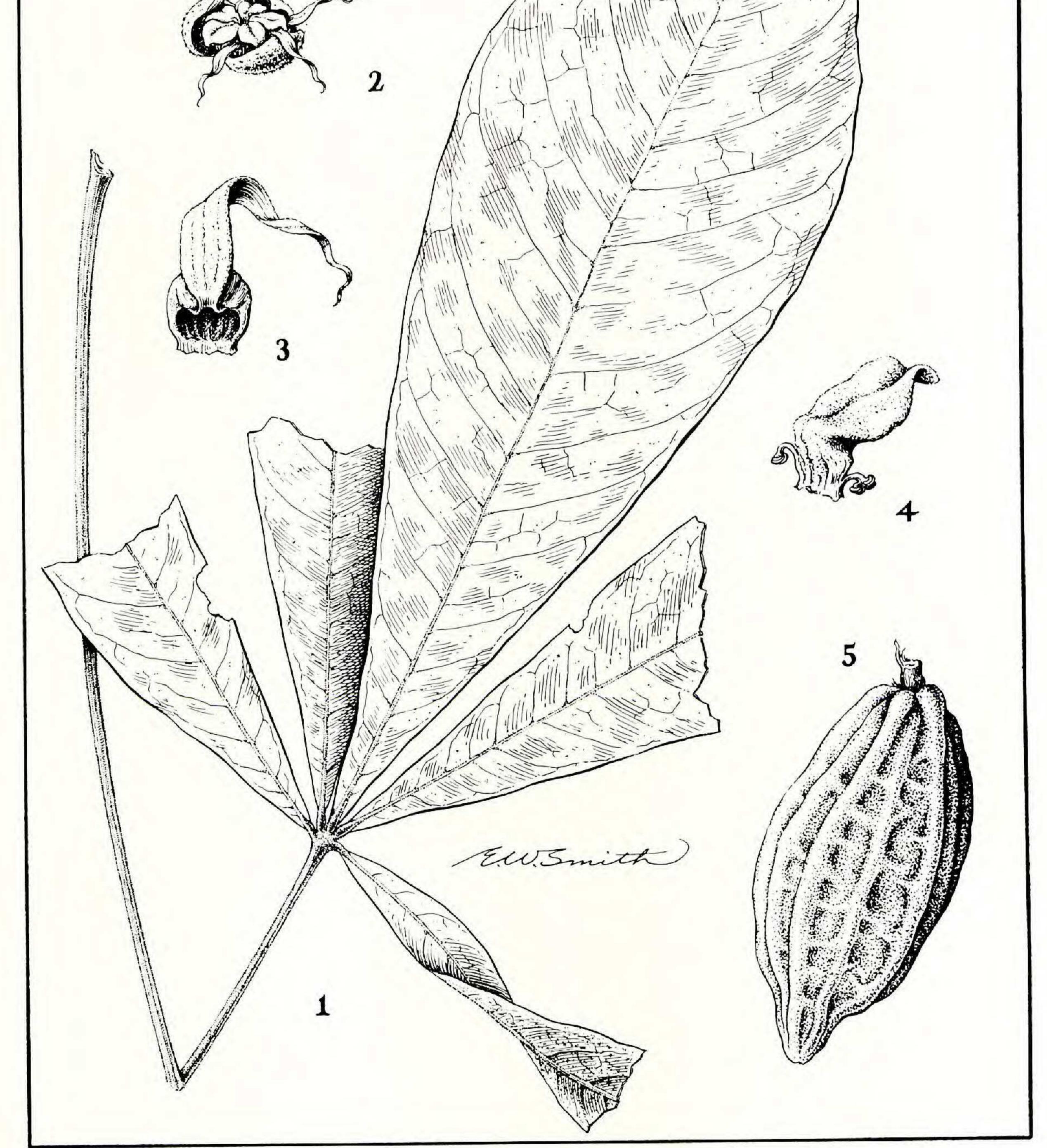
PLATE XVI



Herrania pulcherrima. FIG. 1. Leaf, $\times 1/4$. FIG. 2. Flower, $\times 1/2$. FIG. 3. Petal, $\times 2$. FIG. 4. Staminode and anthers, $\times 2$.

PLATE XVII

HERRANIA purpurea (Pittier) R.E. Schultes



Herrania purpurea. FIG. 1. Leaf, $\times 1/3$. FIG. 2. Flower, $\times 1/2$. FIG. 3. Petal, $\times 2$. FIG. 4. Staminode and anthers, $\times 2$. FIG. 5. Fruits, $\times 1/2$.